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SISTEMAS DE ACASALAMENTO COM DEFESA TERRITORIAL: EVOLUÇÃO, REGRAS DAS DISPUTAS E SELEÇÃO DE TERRITÓRIOS EM SATIRÍNEOS NEOTROPICAIS

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Índice

Resumo

Brigas territoriais entre machos de insetos voadores são resolvidas das mais variadas formas. Em borboletas, existem evidências de que tamanho, idade e motivação são importantes determinantes das chances de vitória. No entanto, as regras utilizadas nas brigas, o contexto biológico que afeta a intensidade dos comportamentos agonísticos e o papel funcional das características dos machos na geração de custos durante os confrontos ainda são pouco conhecidos. Neste trabalho investiguei uma série de características que podem influenciar os custos e benefícios dos confrontos territoriais utilizando as espécies de satiríneos *Hermeuptychia hermes* (Fabricius, 1775), *Moneuptychia soter* (Buttler, 1877) e *Paryphthimoides phronius* (Buttler, 1867) como modelos de estudo. No capítulo 1 investiguei se as disputas intra-específicas pela posse de territórios em machos de *H. hermes* e de *M. soter* ocorrem com contato físico e quais podem ser as características funcionalmente relevantes para a distinção entre machos territoriais e não territoriais. Para tanto, documentei as brigas entre machos utilizando filmagens de alta velocidade e realizei comparações morfológicas e fisiológicas entre machos possuidores de territórios (residentes) e machos que ocuparam territórios nos quais os residentes originais foram removidos (intrusos). Machos residentes de *H. hermes* apresentaram massa corporal e muscular similares às dos seus pares intrusos, porém, possuíram menor desgaste alar e maior quantidade de lipídeos. Machos residentes de *M. soter*, por outro lado, foram mais pesados que os machos intrusos que ocuparam seus territórios. Machos de *H. hermes* podem dividir a interação em vôos circulares, espirais ascendentes e perseguições lineares, enquanto machos de *M. soter* usam vôos circulares mais lentos, os quais são seguidos por perseguições lineares e emissões de som (estalos). Contatos físicos não foram registrados para nenhuma espécie. No capítulo 2 investiguei o papel da residência prévia na resolução de conflitos territoriais entre machos de *H. hermes*. Ao induzir disputas entre dois machos que se comportaram como residentes (um residente original e um

residente induzido) e compará-las com disputas naturais entre machos residentes e intrusos, foi possível demonstrar que a residência prévia aumenta as chances de vitória em um combate. Massa corporal afetou positivamente as chances de vitória nas brigas induzidas, mas não nas brigas naturais. Finalmente no capítulo 3, investiguei a influência da presença de recursos alimentares no estabelecimento de territórios de acasalamento por machos de *P. phronius*. Machos desta espécie defendem sítios de acasalamento localizados em manchas de sol sem recursos evidentes. No entanto, manchas de sol previamente desocupadas passaram a ser defendidas depois de receberem frutas fermentadas. Apesar de machos que se estabeleceram nestes locais aparentemente se alimentarem das frutas, experimentos de escolha de territórios sugerem que eles preferem defender sítios sem recursos e utilizam a defesa de áreas com alimento como tática alternativa de acasalamento. Este estudo representa a primeira investigação deste tipo de variação nas táticas de acasalamento em borboletas. Além de auxiliar a compreensão da evolução de determinados sistemas de localização de parceiros, esse sistema permite testar qual a implicação da existência de mais de uma tática reprodutiva na intensidade dos confrontos territoriais entre machos.

Abstract

Territorial conflicts in flying insects may be resolved through many different ways. In male butterflies, size, age and motivation are often reported as important determinants of the winning chances. However, the rules used when fighting, the biological context that affects the intensity of agonistic behaviors, and the functional role of male traits in the contests costs generation are poorly known. In this study I investigated a series of characteristics that may influence the costs and benefits of territorial conflicts using the satyrine species *Hermeuptychia hermes* (Fabricius, 1775), *Moneuptychia soter* (Buttler, 1877), and *Paryphthimoides phronius* (Buttler, 1867) as study organisms. In chapter 1, I used high-speed video imagery to investigate whether intra-specific disputes between male *H. hermes* and male *M. soter* occur with physical contact. Additionally, I removed resident males from their defended sites and the subsequent intruders that established on those areas after the resident removal to assess if wing wear, body mass, fat content and flight muscle ratio are important determinants of male residency status. Resident males of *H. hermes* were similar in body weight and thoracic muscle mass to their intruder rivals, but had fewer wing wear and higher fat content. Resident males of *M. soter*, on the other hand, were heavier than intruder males. Male *H. hermes* divided their interaction in up to three phases consisting of circular flights, ascending spirals and back and forth persecutions, whereas male *M. soter* used much slower circular flights that were often followed by linear persecutions and clicking sound emissions. Physical contacts were not observed for both species. In chapter 2, I investigated the role of previous residence on contest resolution in the butterfly *H. hermes*. By inducing territorial interactions between males that behaved as residents (one original resident and another resident-induced one) and comparing them with natural contests between resident and intruder males, it was possible to show that previous residence increases the chances of victory. Body mass positively affected the winning chances in the induced fights, but was

unimportant among the natural ones. Finally in chapter 3, I investigated the role of feeding resources in the territory establishment by males of the butterfly *P. phronius*. Male of this species typically defend sunny clearings on the forest edge which do not contain any evident resource. However, previously undefended sunny clearings were occupied by territorial males after receiving soft fermenting fruit. Although males which established on sites containing feeding resources seem to forage on the fermenting fruit, territory selection experiments shows that males prefer to defend sites without resources. This type of variation in the mate locating tactics has never been previously investigated for butterflies. In addition of helping the understanding of the evolutionary processes leading to different mate-locating strategies, this system allows the testing of the influence of different reproductive behaviors on the intensity of territorial conflicts between males.

INTRODUÇÃO GERAL

BRIGAS TERRITORIAIS ENTRE MACHOS

Por que machos brigam?

A busca por parceiros sexuais e o aumento do sucesso reprodutivo são importantes pressões seletivas que favorecem o surgimento de uma série de adaptações morfológicas, fisiológicas e comportamentais tanto em indivíduos do sexo masculino quanto feminino (Thornhill & Alcock 1983; Andersson 1994; Höglund & Alatalo 1995; Shuster & Wade 2003). No entanto, como o investimento dos machos em cada gameta, em geral, é muito menor que o investimento das fêmeas, o aumento do sucesso reprodutivo para indivíduos de cada sexo está associado a fatores distintos (Bateman 1948; Trivers 1972). Para os machos o aumento do sucesso reprodutivo é extremamente dependente do número de fêmeas fertilizadas (Alcock 1979; Bergman et al. 2007). Por outro lado, o sucesso reprodutivo das fêmeas é freqüentemente depende da sua própria fecundidade e da escolha de um único ou de poucos parceiros sexuais de alta qualidade (Bateman 1948; Arnqvist & Nilsson 2000).

Como conseqüência do investimento reprodutivo diferencial, machos quase sempre se encontram sexualmente receptivos, enquanto fêmeas permanecem receptivas por curtos períodos de tempo e se acasalam muito menos freqüentemente (Bateman 1948; Trivers 1972). Esta diferença no período de receptividade sexual acaba tornando machos aptos para acasalamento um recurso muito mais abundante que fêmeas dispostas a se acasalarem (Emlen & Oring 1977). Uma vez que as fêmeas representam um recurso escasso, apenas uma pequena parcela dos machos será capaz de fecundá-las, gerando uma alta variação no sucesso reprodutivo entre indivíduos do sexo masculino. Tal variação, associada à baixa probabilidade de encontro com fêmeas, representa uma forte pressão seletiva sobre os machos no sentido de adquirir parceiras sexuais (Shuster & Wade 2003).

Para aumentar sua taxa de encontro e acasalamento com fêmeas, machos podem empregar uma série de táticas comportamentais distintas que variam desde a busca contínua por fêmeas ao longo de grandes extensões até a defesa de pequenas áreas localizadas em pontos ambientais específicos (Emlen & Oring 1977; Alcock et al. 1978; Parker 1978; Alcock 1980; Thornhill & Alcock 1983; Rutowski 1991). A associação entre as táticas empregadas pelos machos e o número de parceiros que os indivíduos de cada sexo conseguem adquirir define, em última instância, o sistema de acasalamento vigente em cada população (Shuster & Wade 2003).

Apesar da separação dos sistemas de acasalamento em classes distintas não ser adequada para representar toda a variação existente nos meios de aquisição de parceiros sexuais, existe uma grande diversidade de classificações propostas (Shuster & Wade 2003). Porém, de uma forma geral, os sistemas de acasalamento podem ser divididos em quatro grandes categorias (Emlen & Oring 1977): 1) sistemas poligínicos, nos quais uma pequena parcela dos machos em geral consegue fecundar mais de uma fêmea; 2) sistemas poliândricos, nos quais uma fêmea normalmente se acasala com mais de um macho; 3) sistemas promíscuos, nos quais tanto machos quanto fêmeas se acasalam com múltiplos parceiros e 4) sistemas monogâmicos, nos quais machos e fêmeas adquirem somente um parceiro reprodutivo ao longo da vida ou por estação reprodutiva.

Dentro de cada uma dessas quatro grandes categorias, os comportamentos exibidos por machos e fêmeas definem subdivisões do sistema de acasalamento. Especificamente nas espécies poligínicas (e em algumas com sistema promíscuo), os comportamentos dos machos podem definir três subcategorias: poliginia com defesa de recursos, poliginia com defesa de fêmeas e leks (Emlen & Oring 1977; Höglund & Alatalo 1995). Na poliginia com defesa de recursos, os machos defendem algum recurso importante para as fêmeas (tais como locais de alimentação ou oviposição) e cortejam aquelas que visitam o local em busca do recurso (Alcock & Houston 1987; Lederhouse et al. 1992; Carranza 1995). Na poliginia com defesa de fêmeas, machos não defendem diretamente recursos necessários para as parceiras sexuais, mas agrupamentos de fêmeas contra o assédio de outros machos (Gwynne 1980; Bro-Jørgensen & Durant 2003; Kelly 2006). Finalmente nos leks, machos defendem territórios sem qualquer recurso evidente que possa ser utilizado pelas fêmeas (Alcock 1981; Knapton 1985; Svesson & Petersson 1992). Estas visitam os leks exclusivamente em busca de cópulas e abandonam as agregações de machos depois de fertilizadas.

Uma característica particularmente expressiva nos sistemas poligínicos é de que geralmente uma parcela extremamente reduzida dos machos é capaz de monopolizar a esmagadora maioria das fêmeas (Wickman 1985; Blanckenhorn et al. 2003). Nestas situações, a variação no sucesso reprodutivo entre os machos, e conseqüentemente a pressão de seleção, se torna ainda mais acentuada (Shuster & Wade 2003). Como resultado, os machos freqüentemente brigam entre si pela posse das fêmeas, dos recursos utilizados por elas ou das áreas visitadas pelas parceiras sexuais (Baker 1983; Fitzpatrick & Wellington 1983).

As brigas exibidas pelos machos são amplamente variáveis entre as espécies, podendo consistir desde simples exibições sem contatos físicos (Marden & Waage 1990; Kemp et al. 2006) até disputas com contatos físicos intensos e alta probabilidade de morte (Austad 1983; Eberhard 1987). No entanto, apesar das brigas representarem uma interação comum, as regras e os meios pelos quais os rivais decidem o perdedor de um confronto ainda são pouco conhecidas (Taylor & Elwood 2003).

Uma vez que machos brigam, como eles decidem o resultado de um confronto?

Modelos matemáticos baseados na teoria dos jogos forneceram um importante avanço no sentido de formular hipóteses com o intuito de esclarecer as possíveis regras utilizadas pelos machos ao longo de um confronto (Riechert 1998). O primeiro modelo proposto nessa linha (Maynard Smith

& Price 1973) buscava apenas entender porque as disputas raramente causavam injúrias sérias nos oponentes. Porém, este modelo estabeleceu um conceito chave para o entendimento das disputas (e de muitas outras teorias evolutivas) conhecido como estratégia evolutivamente estável. Uma estratégia é dita evolutivamente estável quando, uma vez que ela tenha se fixado em uma determinada população, não poderá ser substituída por nenhuma outra.

A partir dessa proposta, uma série de modelos subseqüentes, cada vez mais adequados a contextos biológicos reais, foram desenvolvidos (Maynard Smith 1974; Maynard Smith & Parker 1976; Bishop et al. 1978; Bishop & Cannings 1978; Parker & Rubenstein 1981; Hammerstein & Parker 1982; Enquist & Leimar 1983; Enquist & Leimar 1987; Mesterton-Gibbons et al. 1996; Payne 1998). O ponto mais fundamental e comum a todos os modelos se refere ao entendimento de como os custos são adquiridos ao longo da interação e quais são as recompensas oriundas da vitória. A partir do estabelecimento das relações de custo-benefício de um confronto, é possível prever quais estratégias comportamentais podem ser mais eficientes nas brigas. Para estabelecer as funções de custo e benefício, todos os modelos compartilham a predição de que as disputas deveriam ser decididas com base em um parâmetro que representa a habilidade de luta de cada rival (RHP – resource holding potential) e em outro parâmetro que representa o valor do recurso disputado. Contudo, a maior diferença entre eles reside na forma como o RHP e o valor do recurso são biologicamente definidos e usados ao longo da interação.

Atualmente, os diferentes modelos sobre regras de disputas entre pares de indivíduos podem ser agrupados em quatro grandes grupos: Guerra de Atritos sem acesso de informação (GDA-SAI), Guerra de Atritos com acesso de informação (GDA-AI), Acesso Seqüencial de Informação (ASI) e Acesso Cumulativo de Informação (ACI). A GDA-SAI (Maynard Smith 1974) presume que as brigas ocorrem sem troca de informações entre os oponentes e que o valor do recurso é igual para todos os rivais. Na guerra de atritos, injúrias não existem, ou caso existam, não devem afetar a persistência dos indivíduos ao longo da interação (Parker 1974). O rival capaz de permanecer na disputa por mais tempo é considerado vencedor. Nesse sentido, o RHP deverá estar relacionado com características que afetem a capacidade de persistência do indivíduo ao longo da interação como, por exemplo, reservas energéticas (Marden & Waage 1990). Como na GDA-SAI cada indivíduo desiste quando atinge um determinado limite de persistência próprio sem avaliar o comportamento ou posição do rival (Mesterton-Gibbons et al. 1996), a duração da disputa deve estar relacionada com o RHP do perdedor, mas não com o do vencedor.

A guerra de atritos com acesso de informação representa uma derivação do modelo de GDA-SAI (Bishop et al. 1978; Bishop & Cannings 1978; Mesterton-Gibbons et al. 1996; Kura & Kura 1998; Haccou & Glaizot 2002). A principal inovação deste modelo está associada à possibilidade de haver avaliação mútua entre os rivais. O modelo de GDA-AI considera que cada rival é capaz de avaliar sua condição (também chamada de papel ou posição) antes da briga, a qual freqüentemente está relacionada com a posse do território (Hammerstein & Parker 1982). Nesse sentido, ao início de um confronto, o indivíduo presente no território pode se considerar como possuidor do recurso disputado (residente) ou como indivíduo mais forte (maior RHP) enquanto o seu oponente como invasor (intruso) ou rival mais fraco (menor RHP). Após esse período de avaliação, cada indivíduo “decide” qual será seu investimento em um confronto. O indivíduo que se considerar em desvantagem, deverá investir pouco ou mesmo desistir do embate caso as assimetrias sejam muito grandes. Tanto a GDA-AI quanto a GDA-SAI presumem que os comportamentos dos rivais não devem variar fortemente em intensidade ao longo da disputa. Entretanto, se há avaliação dos papéis (GDA-AI), quanto menor a assimetria de valor do recurso e RHP entre os rivais, mais longa deverá ser a interação.

Diferentemente dos modelos de GDA, o ASI presume que a avaliação mútua dos rivais ocorre, não no início, mas ao longo da interação (Enquist & Leimar 1983). De acordo com o ASI, os indivíduos adquirem continuamente informações sobre o RHP do rival ao longo da disputa e as usam como uma forma de estimar as próprias chances de vitória. Essas informações são baseadas na média dos comportamentos exibidos ao longo do confronto. Conseqüentemente, quanto mais longa a interação, melhor a estimava do RHP relativo feita por cada oponente. Ao longo da disputa, aquele indivíduo que julgar que o próprio RHP é menor que o RHP do rival, deve desistir do embate. Na proposta original, o valor do recurso supostamente seria igual para ambos os rivais, entretanto, modelos subseqüentes incorporam variações tanto do valor do recurso quanto do RHP (Leimar & Enquist 1984; Enquist & Leimar 1987). Quando esses dois parâmetros podem diferir entre os oponentes, as principais predições do ASI são: 1) quanto maior a similaridade de RHP e valor do recurso entre os rivais, mais longas e custosas serão as brigas; 2) quando as disputas possuem fases distintas, etapas subseqüentes devem ser mais custosas que as etapas anteriores (mas cada etapa deve apresentar um custo relativamente constante); e 3) baseado na premissa de que informações mais precisas são fornecidas a partir de comportamentos mais custosos, estes deveriam ser usados somente quando os oponentes apresentarem alta simetria de RHP e valor do recurso.

O terceiro modelo (ACI), proposto por Payne (1998), parte da premissa de que os animais são capazes de causar injúrias nos seus adversários (Parker 1974) e, conseqüentemente, podem basear suas decisões de permanência em um confronto avaliando a soma dos próprios custos adquiridos ao longo da briga (Payne & Pagel 1996; Payne & Pagel 1997). De acordo com o ACI, não há aquisição de informação sobre RHP do oponente. A decisão de permanência depende do próprio indivíduo, o qual teria um limite máximo de dano que ele é capaz de acumular antes de desistir do confronto. A principal predição desse modelo é de que o RHP deve depender da interação entre a resistência a danos e a quantidade de injúrias recebidas. Os vencedores de uma disputa deveriam iniciar o confronto com uma maior intensidade ou freqüência de exibição de comportamentos agonísticos, mas apresentarem uma taxa de aumento menos intensa desses comportamentos ao longo da interação quando comparados com os perdedores.

Apesar do grande avanço nos modelos propostos para o entendimento das disputas, poucos estudos empíricos foram capazes de testá-los simultaneamente (Taylor & Elwood 2003; Kelly 2006; Stuart-Fox 2006; Kemp et al. 2006; Briffa 2008). A principal dificuldade para o teste de tais modelos reside na criação de premissas exclusivas a cada um ou que compreendam as variações que podem existir dentro de um mesmo modelo (Taylor & Elwood 2003; Stuart-Fox 2006). Além disso, como todos os modelos se baseiam em relações de acúmulo de custos que dependem do RHP e da disposição ou investimento que cada rival fará no confronto (valor do recurso), é fundamental identificar as características determinantes do RHP e do valor do recurso antes que os modelos possam ser efetivamente testados.

Diversos fatores são potencialmente relevantes na determinação dos custos e dos benefícios das disputas (Fig. 1). Em particular, aspectos como as taxas de acasalamento, existência de eventuais estratégias reprodutivas alternativas e características dos sítios defendidos são especialmente relevantes para a determinação dos benefícios de uma disputa. Com relação aos custos, os comportamentos empregados ao longo do confronto e as características determinantes do RHP são de especial importância.

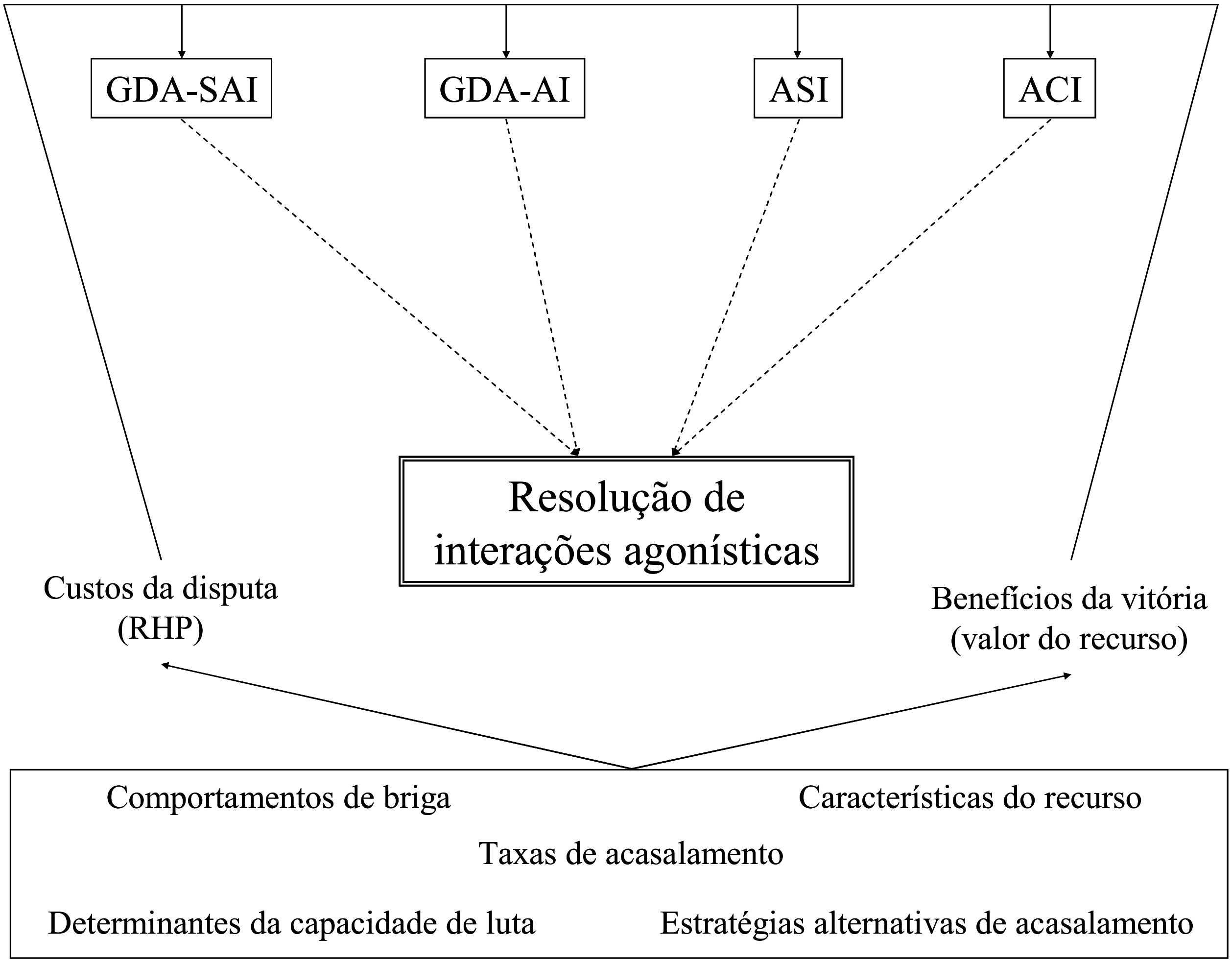

Figura 1. Modelo esquemático indicando as principais informações necessárias para que os custos e os benefícios das disputas possam ser estimados. A partir destas estimativas, testes efetivos das principais regras utilizadas por pares de machos na resolução de disputas poderão ser realizados. GDA-SAI – guerra de atritos sem acesso de informação; GDA-AI – guerra de atritos com acesso de informação; ASI – acesso seqüencial de informação; ACI – acesso cumulativo de informação.

As taxas de acasalamento, as características do recurso defendido e a existência de eventuais estratégias alternativas de encontro de parceiros permitem avaliar os benefícios reprodutivos ao vencer um confronto e contrapô-los com os benefícios ganhos ao adotar comportamentos não agressivos. Por exemplo, em algumas espécies machos mais fortes podem adquirir fêmeas por vias que não necessitam de lutas pela posse de territórios, enquanto machos mais fracos conseguem adquirir parceiras sexuais somente ao defenderem algum sítio de acasalamento. Nestes casos, machos mais fracos podem atribuir maior valor ao recurso defendido e vencer a disputa contra indivíduos presumivelmente mais fortes (Hernández & Benson 1998).

Os comportamentos empregados ao longo de um confronto e as características determinantes da capacidade de luta, por sua vez, são importantes para que seja possível identificar os principais custos de uma briga e esclarecer como eles são adquiridos ao longo da mesma. Nesse aspecto, é importante salientar que a simples identificação de características morfológicas ou fisiológicas associadas a indivíduos vitoriosos ou perdedores não assegura o correto estabelecimento dos determinantes da capacidade de luta (Austad 1983; Eberhard 1987; Alcock 1993; Adamo & Roy 1995; Alcock & Bailey 1997; Fitzstephens & Getty 2000; Coelho & Holliday 2001; Briffa & Elwood 2001; Briffa 2008). Correlações espúrias entre caracteres associados ao RHP e caracteres não relacionados ao acúmulo de custos podem levar a conclusões equivocadas sobre o papel de algumas características na resolução dos conflitos. Para assegurar a correta identificação dos fatores relevantes para a determinação da habilidade de luta, é importante esclarecer qual a relação funcional entre os caracteres dos machos e a sua função na disputa (Lailvaux & Irschick 2007). Nesse sentido, uma investigação detalhada dos comportamentos adotados ao longo de um confronto é essencial para que essas relações funcionais possam ser estabelecidas.

Entre os artrópodes é possível dividir os confrontos em dois grandes grupos comportamentais: disputas sem contato físico e disputas com contato físico. Se uma disputa ocorre com contato físico, injúrias diretas são potencialmente importantes para a resolução do conflito, pois podem representar o principal meio pelo qual os custos são adquiridos ao longo da interação (Eberhard 1987; Buzatto & Machado 2008). Neste sentido, a capacidade de luta de cada indivíduo pode ser definida pela sua habilidade de causar ou evitar danos, pela sua resistência a injúrias ou por uma combinação dos dois. Por outro lado, se disputas ocorrem sem contato físico, injúrias propriamente ditas são improváveis (Takeuchi & Imafuku 2005). Um indivíduo ainda pode ser capaz de reduzir a aptidão do seu rival se, ao longo da interação, for possível forçar mudanças nas taxas metabólicas do inimigo e conseqüentemente reduzir suas reservas energéticas ou mesmo causar acúmulo de resíduos metabólicos (Briffa & Elwood 2005). Porém, disputas decididas simplesmente por capacidade de persistência sem efeitos gerados pelos rivais são muito mais prováveis em interações sem contato físico (Marden & Waage 1990; Mesterton-Gibbons et al. 1996).

Por que estudar borboletas?

Praticamente todas as espécies de borboletas territoriais estudadas até o momento exibem disputas que ocorrem principalmente durante o vôo (Kemp & Wiklund 2001; Chaves et al. 2006). Insetos que brigam pela posse de territórios de acasalamento usando brigas aéreas constituem um sistema interessante para o teste dos modelos sobre as regras e a evolução de interações agonísticas. Uma vez que machos interagem durante o vôo, contatos físicos com possíveis injúrias tendem a ser raros (Kemp & Wiklund 2001; Peixoto & Benson 2008). Contudo, em casos isolados tais contatos podem ser importantes para a resolução dos conflitos (Eff 1962; Pinheiro 2001; Chaves et al. 2006). Apenas uma pequena parcela das espécies que disputam territórios de acasalamento utilizando confrontos durante o vôo apresenta estudos detalhados acerca da sua história natural e das características importantes para resolução das disputas (Alcock et al. 1978; Baker 1983; Fitzpatrick & Wellington 1983; Alcock 1987a; Wickman & Rutowski 1999; Kemp & Wiklund 2001; Córdoba-Aguilar & Cordero-Rivera 2005). Em particular, nenhuma espécie que ocorre no Brasil chegou a ser profundamente investigada nesse aspecto.

Borboletas são tão interessantes como modelo de estudo quanto qualquer outro grupo de artrópodes. Porém, questões distintas são mais facilmente respondidas utilizando grupos distintos como modelos. Vespas, abelhas, borboletas e libélulas representam os grupos que concentram a maioria dos estudos sobre interações agonísticas e suas regras de resolução em insetos voadores (Alcock 1975; Alcock et al. 1978; Baker 1983; Fitzpatrick & Wellington 1983; Kemp & Wiklund 2001; Córdoba-Aguilar & Cordero-Rivera 2005; Kemp & Alcock 2008; Peixoto & Benson 2008).

Entre as libélulas, reservas energéticas e infestação por parasitas parecem ser os principais fatores que afetam a habilidade de luta dos machos (Marden & Cobb 2004; Córdoba-Aguilar & Cordero-Rivera 2005; Contreras-Garduño et al. 2006; Contreras-Garduño et al. 2008). Com relação ao valor do recurso, é possível distinguir dois grupos: um no qual os machos territoriais aparentemente não utilizam nenhum recurso evidente como pista para o estabelecimento dos territórios (Johnson 1962; Alcock 1982; Peixoto & De Marco Jr. 2009) e outro nos quais os machos defendem territórios que nitidamente contém agregações de recursos utilizados pelas fêmeas (Alcock 1987b; 1990; Marden & Rollins 1994). Para este segundo grupo, os principais recursos que afetam o valor do território são a presença de macrófitas aquáticas, velocidade da correnteza e freqüência de encontro com fêmeas (Alcock 1987b; Meek & Herman 1991; Gibbons & Pain 1992).

Em vespas e abelhas, reservas energéticas nunca foram relatadas como determinantes da capacidade de luta. Nesse grupo é relativamente comum a ocorrência de espécies que brigam tanto por interações sem contatos quanto outras nas quais contatos físicos são intensos (Alcock et al. 1978; Alcock 1980; Alcock & Houston 1996). De forma geral, machos maiores tendem a vencer as disputas. Entretanto, apesar do tamanho claramente conferir vantagem na subjugação de rivais menores em brigas com contato físico, sua função nas disputas sem contato ainda é obscura (Kemp & Alcock 2003; Kemp & Alcock 2008). Com relação às características importantes para o estabelecimento dos territórios, novamente o padrão é bastante variável (Alcock 1975; Alcock et al. 1978; Alcock 1980). Algumas espécies defendem pequenos territórios sem recursos evidentes localizados em topos de morro, outras defendem recursos alimentares utilizados pelas fêmeas, locais de emergência, recursos necessários à construção do ninho ou podem até mesmo apresentar mais de um sistema territorial em uma mesma população (Groddeck et al. 2004). Porém, investigações sobre a importância de tais características na valorização do território são raras.

Finalmente para borboletas, existe uma alta variação nas características importantes para resolução dos conflitos (Kemp & Wiklund 2001; Peixoto & Benson 2008). Revisões passadas sugeriram que machos que retêm territórios de acasalamento claramente têm maior habilidade de luta que machos que não possuem territórios (Kemp & Wiklund 2001). Entretanto, os fatores determinantes da habilidade de luta são pouco conhecidos. Tamanho inicialmente não foi considerado como um candidato que possa afetar funcionalmente o RHP. Contudo, recentemente foi demonstrado que machos maiores ou mais pesados claramente possuem vantagens nas disputas para pelo menos metade das espécies estudadas até o momento (Peixoto & Benson 2008). Idade também é freqüentemente relacionada com a habilidade de luta, havendo espécies nas quais machos mais novos têm maior RHP e espécies nas quais este padrão é invertido (Kemp 2005). Contudo, o papel funcional destas características na geração de custos ao longo do confronto ainda é desconhecido. Fatores que afetam o valor do recurso são pouco conhecidos em borboletas, principalmente por que para muitas espécies as características que definem os territórios são obscuras e de difícil identificação (Alcock & Gwynne 1988; Lederhouse et al. 1992; Kemp & Rutowski 2001; Ide 2004; Takeuchi & Imafuku 2005).

E quanto a esta tese?

Ao longo do mestrado iniciei a descrição do contexto biológico necessário para o teste de hipóteses referentes às regras de resolução de confrontos territoriais para a espécie de borboleta *Paryphthimoides phronius* (Butler 1867). O presente trabalho nada mais é que uma continuação dos estudos iniciados no mestrado, mas no qual foi possível estabelecer mais claramente os fatores que levaram ao surgimento e manutenção do comportamento territorial.

Esta tese representa um estudo com duração de aproximadamente 300 dias de campo distribuídos ao longo de dois anos e meio de coletas. Entretanto, como nem todas as espécies representam modelos adequados para diferentes experimentos, utilizei três espécies, com graus de conhecimento distintos, para testar algumas hipóteses sobre a evolução dos sistemas de acasalamento e sobre as regras utilizadas para a resolução das interações agonísticas entre machos. As espécies utilizadas foram: *Hermeuptychia hermes* (Fabricius, 1775), *Moneuptychia soter* (Butler, 1877) e *Paryphthimoides phronius* (Fig. 2).

Figura 2. Macho marcado de *Hermeuptychia hermes* (A), macho marcado de *Moneuptychia soter* (B) e macho de *Paryphthimoides phronius* (C).

O trabalho está dividido em três capítulos que resumem as principais descobertas feitas ao longo do doutorado. Alguns dos experimentos que desenvolvi representam tentativas inéditas para borboletas, que por terem sido realizadas pela primeira vez, obviamente apresentam méritos e problemas. Adicionalmente, muitas das informações contidas aqui representam a primeira descrição de determinados fenômenos para lepidópteros. Tais informações são importantes, pois nos permitem melhorar nossa compreensão sobre os possíveis mecanismos envolvidos na resolução de conflitos entre machos e os processos subjacentes a evolução de diferentes sistemas de acasalamento em insetos. No capítulo 1, utilizei filmagens de alta velocidade para descrever os comportamentos agonísticos exibidos por machos de *H. hermes* e *M. soter* durante as disputas pela posse de sítios de acasalamento. Adicionalmente, realizei comparações experimentais entre machos que possuíam territórios e machos que ocuparam áreas nas quais machos territoriais foram removidos para avaliar possíveis diferenças morfológicas e fisiológicas relacionadas com as chances de vitória em um confronto. No capítulo 2, testei se a ocupação prévia de um território pode aumentar as chances de vitória dos machos. Posteriormente, testei se ao longo do confronto, os rivais podem desistir de um combate baseados em auto-avaliação ou em avaliações mútuas da habilidade de luta. No capítulo 3, avaliei se machos podem usar frutas em decomposição como pista para o estabelecimento de territórios de acasalamento e se esta tática é preferencialmente adotada quando comparada com a defesa de sítios que não possuem recursos alimentares em abundância.

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CAPÍTULO 1

Relating fighting ability indicators with fight behavior in two tropical satyrine butterflies

Relating fighting ability indicators with fight behavior in two tropical satyrine butterflies

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Abstract: In insect species that dispute the ownership of mating sites via aerial interactions, there is little consensus about which morphological and physiological traits are related to territorial success and how each trait functionally translate into costs during a fight. Among butterflies, size, weight and age seem to be the main candidates influencing male fighting ability. However, since detailed descriptions of the behaviors adopted during contests are rare, it is difficult to infer how these traits functionally affect male RHP and the costs of fighting. In this study we used high-speed video recording (240 frames per second) to provide a detailed description of the fighting behaviors in two previously unstudied small satyrine butterflies: *Hermeuptychia hermes* (Fabricius, 1775) and *Moneuptychia soter* (Butler, 1877). Additionally, we performed removal experiments to assess if wing wear, body mass, fat content and flight muscle ratio are important determinants of male residency status. Based on the fighting structure, we also inferred how those traits might affect the chances of victory during a territorial interaction. We filmed a total of 23 fights in *H. hermes* and 10 in *M. soter*. Males of *H. hermes* could divide the interaction in circling, ascending spiraling and back and forth aerial persecutions, while males of *M. soter* used much slower circling flights that often finished with linear chases accompanied by clicking sound emissions. Although these two species disputed mating sites using very different behaviors, apparently neither employed physical contact to settle contests. In *H. hermes* younger males with greater fat content accumulated in the resident role (n=26 pairs), suggesting that males of this species may compete via "endurance contests". On the other hand, resident males of *M. soter* were heavier than replacements (n=11 pairs), but did not present differences in any other measured trait. Since disputes occurred without physical contact, it is difficult to imagine how mass or size may functionally affect the chances of victory. Weight may be related to other unmeasured traits such as condition, parasitic load or even specific aerodynamic designs related to flight speed or maneuverability.

INTRODUCTION

The competition among males to increasing access to sexual partners is one of the major forces driving the evolution of a wide variety of behavioral, morphological and physiological traits in animals (Andersson 1994; Shuster & Wade 2003). Males mating tactics vary from non-interactive processes, such as continuous searching for receptive females to the contest defense of mating areas that have greater chances of encountering receptive mates. Among insects, the territorial defense of mating areas is widespread. Although it is common to observe males disputing the possession of these sites, there is much controversy about which factors are responsible for male success in territorial disputes and how costs are accrued during a fight (Baker 1983; Fitzpatrick & Wellington 1983; Kemp & Wiklund 2001).

Theory regarding animal contests proposes that male-male agonistic interactions should be settled in favor of the individual with higher fighting ability (RHP – resource holding potential) or that places higher value on the disputed resource (RV – resource value) (Parker 1974; Bishop & Cannings 1978; Enquist & Leimar 1983; Mesterton-Gibbons et al. 1996). In this sense, to be able to understand the rules used to decide the winner of a dispute, it is necessary to identify how individual traits affect fighting ability and how the interaction between environmental and biological factors influences territory value.

The conspicuousness of interactions and the presence of exaggerated male traits make the identification of characteristics associated with RHP straightforward in some species (Pratt et al. 2003; Kelly 2006). However, in species that compete via aerial fights, such as odonates, butterflies, dipterans and wasps, the identification of these traits is frequently much less certain (Kemp & Wiklund 2001; Preston-Mafham 2001; Kemp & Alcock 2003; Contreras-Garduño et al. 2006). Among candidate traits, size, weight, age, fat reserves and immune ability seem to predominate (Alcock et al. 1978; Kemp & Wiklund 2001; Córdoba-Aguilar & Cordero-Rivera 2005). However, due to existence of potential correlated traits, the main puzzle is to establish functional causal links between male characteristics and the chances of victory (Lailvaux & Irschick 2007). In especial, it is difficult to establish the processes relating the traits linked to winner or loser males and their function in the mechanisms of cost accumulation along the interactions.

As a first step, a detailed examination of fight structure is of fundamental importance to understand how each trait may influence male success in contests (Lailvaux & Irschick 2007; Kemp & Alcock 2008). For example, for species which males grapple in the air (Alcock & Houston 1987; Pinheiro 2001), physical strength is probably involved and size or mass should be related to imposing costs on opponents. In the case of aerial combat, maneuverability may also be important by increasing the effectiveness of contact between rivals and avoidance of collisions with vegetation and other obstacles (Kemp & Wiklund 2001; Kemp 2003). On the other hand, if there is no physical contact between males, there is little reason to expect weight (in itself) to be causally related to contest success. In these situations, characters that favor endurance, such as fat reserves and perhaps youth, may increase male RHP (Marden & Waage 1990; Marden & Rollins 1994).

Males of many butterfly species compete for the possession of mating sites through elaborate aerial maneuvers (Kemp & Wiklund 2001). Although disputes often occur without apparent physical contact, which indicate that fat reserves should be important in determining a male fighting ability, there is great uncertainty about which male traits are relevant to contest resolution. Many species do not show clear morphological or physiological differences between winner and losers. For the species which show some difference, size and body mass seem to be important in many cases (Peixoto & Benson 2008), whereas in others, age (wing wear) also affects contest outcome (Kemp 2000; Kemp et al. 2006b). Although little examined, traits that might affect endurance (such as fat reserves) and maneuverability (such as the ratio of thoracic muscles to body mass), seem to play a minor role in butterfly territorial interactions (Kemp 2005;

Takeuchi 2006; Kemp et al. 2006a; Kemp et al. 2006b). However, since few detailed descriptions of butterfly contest dynamics exist (Wickman & Wiklund 1983; Takeuchi & Imafuku 2005), our capacity to evaluate how traits might affect male RHP is limited.

In this study, we used high-speed video imagery to investigate the territorial disputes of two previously unstudied tropical satyrinae species: *Hermeuptychia hermes* (Fabricius, 1775) and *Moneuptychia soter* (Butler, 1877). Our main objectives were to provide detailed descriptions of male disputes in these morphologically similar species and, based on the fight structure, investigate how morphological and physiological traits might affect the chances of a male to win a territorial dispute.

METHODS

Study Species

Hermeuptychia hermes is a small dull brown butterfly (mean wing length ± SD, 1.74 ± 0.08 cm, n=56 males) commonly found along forest edges and fields year round. Depending upon the area, this species may show a scramble competition mating system (sensu Emlen & Oring 1977), or have males defending specific mating sites along forest edges between 11:00 and 16:00 h (Peixoto et al. *in prep*). The territories used by males consist of small sunny gaps (c. 5 m diameter) on forest edges, often located at the entrance of small trails.

Moneuptychia soter is predominantly gray and slightly bigger than *H. hermes* (mean wing length ± SD, 1.79 ± 0.05 cm, n=28 males). This species flies mainly between October and March, when males are observed defending territories between 11:00 and 13:00 h in sunny clearings located into the forest at about 5 m from the forest edge. They often perch 3-4 m high on trees slightly smaller than the surrounding vegetation from which they fly out to intercept passing insects.

Study Area

The study was undertaken at approximately 1000 m elevation in the Environmental Protection Zone of the Serra do Japi, a network of wooded ridges near the city of Jundiaí, São Paulo State, Brazil (23^{o}14’S; 46^{o}56’W). This area has approximately 35,400 ha and a mean annual temperature of 15.7 ^{o}C. The rainy period extends from September to March and the dry period from April to August (Pinto 1992). The main study area, 150 m in length, was located along an unpaved road inside the reserve. Males of *H. hermes* defended up to seven different territories in the study area and three additional ones were also observed about 1 km away. Males of *M. soter* defended three territory sites within the main area (none of which were used by male *H. hermes*).

Territorial disputes recording

In order to document male behavior during territorial disputes, we recorded, between September 2007 and April 2008, 23 interactions involving males of *H. hermes* and 10 interactions involving males of *M. soter* using a high speed video-camera (Sony Handycam – HDR-SR7). This equipment was able to record a series of three second blocks at 240 frames per second. In this sense, for each paired interaction we recorded as many blocks as possible [mean ± SD (min-max): *H. hermes* = 3.57 ± 4.02 (1-17) blocks/dispute; *M. soter* = 4.40 ± 2.27 (1-7) blocks/dispute]. Afterwards, we examined each recording frame by frame in order to identify behavioral sequences used during the dispute and to evaluate the degree of body contact in each species.

Removal experiment

Between March and June 2006 for *H. hermes* and October 2007 and April 2008 for *M. soter*, we removed resident males from territories and recorded how long, to the nearest minute, it took for a new-comer male (substitute male) to arrive and begin to defend in the same place. Only males that we observed repeatedly flying at a specific area inside the focal territory or defending it (against other males or other insect species) during at least one minute were included in this experiment. After the removal, we captured each substitute male that subsequently settled in the territory on the same day and then measured all butterflies for several morphological and physiological traits (see the topic "morphometric measurements" for a detailed description of the measured traits). Whenever more than one new-comer male established in the same territory after the original resident removal, we averaged trait values among the substitute individuals. For *M. soter*, we always removed the resident males between 11:10 and 11:30 h and waited for a new-comer occupation until 12:45 h. For *H. hermes*, we removed the original residents between 12:00 and 13:00 h and waited for a substitute arrival until 15:00 h.

We used multiple logistic regression to evaluate the effect of male traits on the probability of being a primary resident (Hosmer & Lemeshow 1989). However, since our experiment was paired, we randomly ascribed focal status to the primary resident (focal status 1) in half the removals and to substitute males in the other half (focal status 0) to perform the multiple logistical regression. For each pair, we calculated the difference in all measured traits as the value for the focal individual minus the value for its "rival". This procedure tested the probability of victory of a focal male in relation to the signed difference in trait values from those of its rival. Additionally, to select the most parsimonious model describing the relationship between focal male status and the difference in trait value from its rival, we used an information theoretic approach. We selected the model that minimized the bias-corrected version for small samples of the Akaike Information Criterion (AIC_c) as the most parsimonious candidate model (Burnham & Anderson 2002). We performed all statistical analyzes using the R program (R Development Core Team 2004, http://www.R-project.org).

Morphometric measurements

We measured a total of four traits in each male: body weight, wing wear, fat content, and thoracic muscle mass. Wing wear and weight were measured in the field immediately upon capture. After these measurements, all individuals were placed in a box with ice and transferred to a refrigerator where they were maintained until extracted for fat and thoracic muscles in the lab.

We estimated wing wear on a three scale point: individuals with soft wings and no scale loss were classified as young (rank 0); individuals with hard wings and little scale loss as intermediate (rank 1) and individuals with hard wings, much scale loss and wing damage as old (rank 2). Afterwards, we transferred each male to a small pre-weighed envelope for weighing on a portable balance (Pocket-Pro® model PP-2060D, sensitivity 1 mg).

To estimate absolute fat content and thoracic muscle dry mass, we first dried males at approximately 70 ^{o}C for 96 h. We measured dry thorax (without wings and legs) and abdomen of each individual with a Can C-30 microbalance (precision 10^{-5} mg). Afterwards, we enclosed the male body parts in a vial containing 5 ml chloroform for 48 h. After this period, we dried the extracted body parts for an additional 96 h and re-weighted them. We calculated the fat content as the weight difference before and after the extraction in chloroform. To test the efficiency of this method, we took a sub-sample of 10 extracted male butterflies and repeated the procedure a second time. This test revealed that no additional weight loss occurred in either *H. hermes* (paired t-test, t=0.45, df=9, p=0.664) or *M. soter* (paired t-test, t=1.15, df=9, p=0.279). Muscle mass was calculated as above. However, we used the difference in fatless thoracic weight before and after its immersion in 10 ml of 0.35 M sodium hydroxide for 72 h as our measure of dry thoracic muscle mass (Marden 1987).

In order to obtain values of fat content independent of male size, we used the standardized residuals of regressions between fat content on fatless body mass for both *H. hermes* and *M. soter*. Similarly, we used the standardized residuals from the regressions between thoracic muscles and total dry body mass as size independent values of flight muscle ratio - FMR (Marden & Chai 1991; Marden & Rollins 1994). For the logistic regressions involving *H. hermes*, we used all measured traits. However, due to the small sample size for *M. soter*, we omitted wing wear because data were very homogeneous (six pairs did not differ in wing wear and four differed in just one unit).

RESULTS

Territorial disputes recording

Contests between male *H. hermes* consisted of up to three sequential phases: initial contact flight, circling or spiraling pursuits and linear chases. With the intruder approximation into a defended site, the resident male generally flew to confront it, resulting in a brief circular flight within or near the territory (first phase). Non-filmed observations indicate that the disputes often terminated during this phase, but in a few cases the circular flights were followed by upward spiral pursuits that could reach 15-20 m high. However, in some cases, rather than spiraling upwards, the fighting pair engaged in circular flights near the ground (approximately 1 m high). Both circular and spiraling flights could take the disputing pairs for far outside the territory boundaries. During these chases, males repeatedly changed the flight direction between clockwise and counterclockwise. Among the 23 videotaped disputes, two broke-off in the first phase (8.6%), 17 (73.9%) escalated to the upward spiral phase and four (17.4%) to the circular flight near the ground. Sometimes, rivals would separate, ending an interaction, and return to the territory where they initiated another series of circular or spiraling flights. In the third phase (n=21), males engaged in a linear aerial pursuit (winner male pursuing the looser) that extend far from the territory site. We recorded just two fast contacts between rivals (duration of approximately 0.125 sec). These contacts were apparently occasional and did not cause any evident deviations in the male flight trajectories. However, it was not possible to identify if the contacts involved just wings or other body parts.

Males of *M. soter* flew visibly slower than *H. hermes* during disputes. The disputes among *M. soter* males were very similar among pairs, usually divided into an initial circular phase and a final linear persecution. An interaction often began when a resident flew towards an intruder approaching the territory. At this point, they could spend just a few seconds in a circular flight before terminating the interaction or continuing circling for many minutes (due to the video recording methods, we were unable to time the exact duration of disputes). During this phase, males repeatedly changed flight direction between clockwise and counterclockwise. After the circular flight phase, males typically changed to linear back and forth persecutions until the looser flew off and the winner returned to the territory. During the linear chases (and sometimes at the beginning of the interactions), it was possible to hear sharp clicking sounds emitted by rivals (we were unable to identify if the sound was emitted by one or both males). Males frequently flew short distances outside and into the territory boundaries during both the circular and linear phases. We never observed physical contacts between rivals in video sequences or during direct observations.

Removal experiments

We removed 36 resident males of *H. hermes* from their territories. In 26 of these, a new-comer male occupied the territory and was successfully captured (in two trials there were two intruder males). The mean elapsed time between the removal of the resident male and occupation by a second individual was 34.6 (n=25, SD=25.7) min (Fig. 1). Substitute males typically occupied an induced vacant territory between one and 40 min, but on rare occasions, it could take as long as 140 min to occupy a mating site.

Resident males of *H. hermes* tended to present higher fat content than substitutes, but very similar total body weight and thoracic muscle mass (Table 1). The logistic model with all predictor variables included (body weight, wing wear, flight muscle ratio and residual fat content) indicated a strong relationship between the probability of residency and the trait differences between rivals (AIC_c=33.7, χ^2=15.36, p=0.004). However, the most parsimonious candidate contained only age (wing wear) and residual fat content differences as predictor variables (AIC_c=29.2, χ^2=13.98, p<0.001). Younger males with greater residual fat content tended to concentrate in the resident role while older individuals with less residual fat content in the substitute position (Figs. 2 and 3).

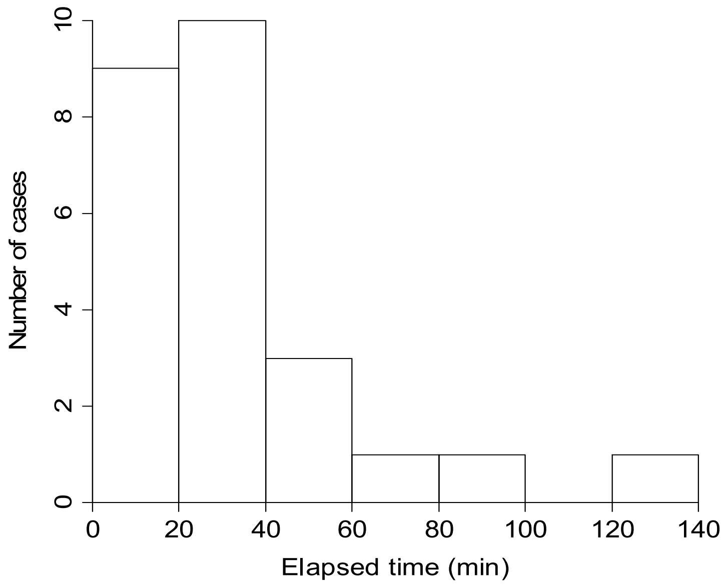

Figure 1. Frequency distribution of elapsed times between the removal of a resident male of *Hermeuptychia hermes* and the new-comer arrival at the focal territory.

Table 1. Mean trait values for resident and intruder males of *Hermeuptychia hermes* and *Moneuptychia soter*. Non-paired data indicate the absolute mean values for resident and intruder males. Paired data indicate mean values for the difference between the focal male and its rival. Values in parentheses indicate the standard deviation. The sample size for *M. soter* is 11 resident and 11 intruder males for the non-paired data and 11 pairs for the paired data. The sample size for *H. hermes* is 26 resident and 28 intruder males for the non-paired data and 26 pairs for the paired data.

Species	**Data**	**Status**	**Wing wear index**	**Fat content (mg)**	**Body weight (mg)**	**Thoracic muscles (mg)**
M. soter	Non-paired	Resident	1.67 (0.78)	0.92 (0.26)	26.67 (2.23)	2.69 (0.32)
		Intruder	1.92 (0.90)	0.78 (0.27)	24.58 (2.02)	2.53 (0.28)
	Paired	Resident	0 (0.71)	0.08 (0.76)	1.20 (2.59)	1.20 (1.53)
		Intruder	0.33 (1.03)	-0.20 (0.78)	-2.33 (2.25)	-0.19 (1.80)
H. hermes	Non-paired	Resident	1.35 (0.59)	0.67 (0.23)	22.75 (2.29)	1.85 (0.30)
		Intruder	1.88 (0.85)	0.54 (0.17)	21.64 (3.08)	1.83 (0.40)
	Paired	Resident	-0.07 (1.04)	0.23 (1.04)	0.002 (0.003)	0.26 (1.30)
		Intruder	0.88 (0.77)	-0.73 (0.94)	-0.0002 (0.003)	-0.42 (1.30)

*For the non-paired data we used the absolute values of fat content, weight and thoracic muscles. For the paired data we used the standardized residuals for fat content and thoracic muscles (see methods for a detailed description of how we obtained the standardized residuals).

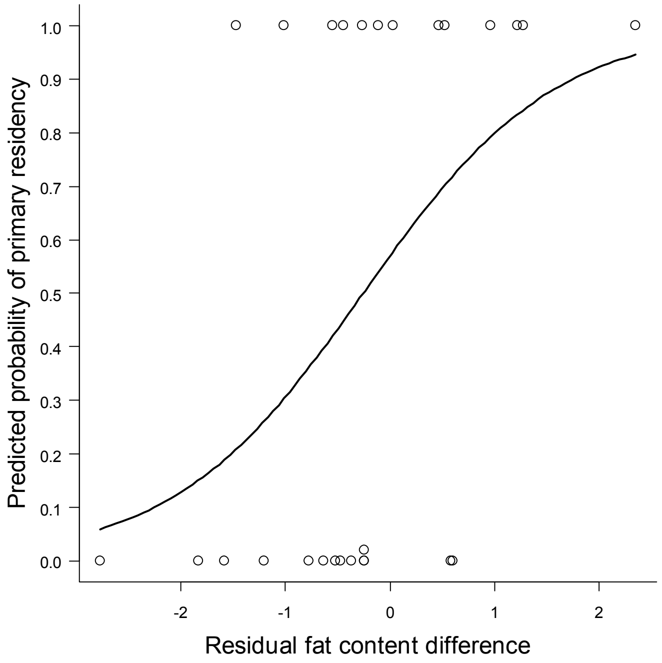

Figure 2. Predicted probability of a male of *Hermeuptychia hermes* to be in the resident role in relation to the difference in residual fat content from its rival. Superimposed points represent different samples with the same focal result and weight.

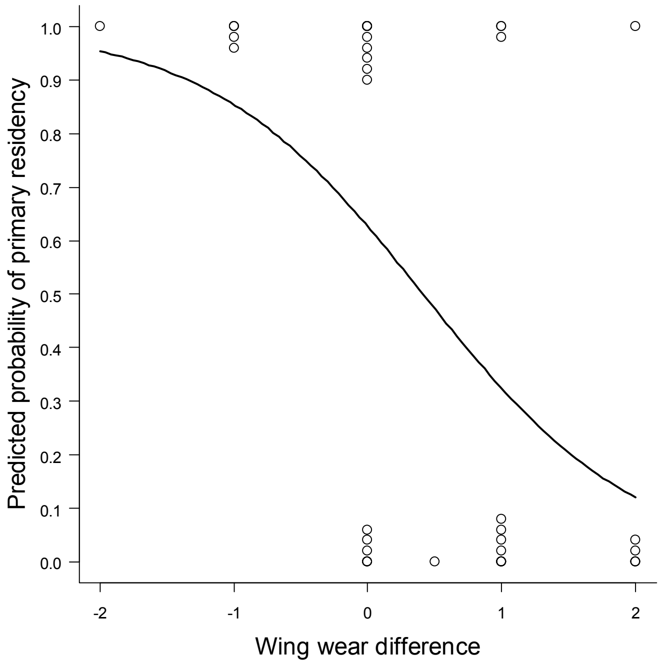

Figure 3. Predicted probability of a male of *Hermeuptychia hermes* to be in the resident role in relation to the age difference from its rival. Superimposed points represent different samples with the same focal result and weight.

We removed 34 resident males of *M. soter*, but only 11 territories were subsequently occupied by a substitute individual (all occupations were performed by just one substitute male). The mean time between the resident removal and arrival of the new-comer was 19.4 (SD=10.6) min (Fig. 4). The substitute male occupied the vacant territory within 20 min in approximately 55% of the removals. The maximum time elapsed before the new-comer male arrived was 40 min, much less than the maximum time registered for *H. hermes* males.

Resident males of *M. soter* tended to be heavier and fatter than substitute ones, but did not differ in thoracic muscle mass (Table 1). Although the complete logistic model suggested a marginally significant relationship between the chances of a male to be the primary resident in relation to the traits difference from the non-focal individual (AIC_c=22.9, χ^2=6.92, p=0.07), the most parsimonious candidate included only weight difference as a significant predictor variable (AIC_c=15.3, χ^2=5.37, p=0.02). Heavier males were preferentially found in the resident role, while lighter males in the substitute one (Fig. 5). It is interesting to note that weight differences among males of *M. soter* were much more variable than the values observed for males of *H. hermes*.

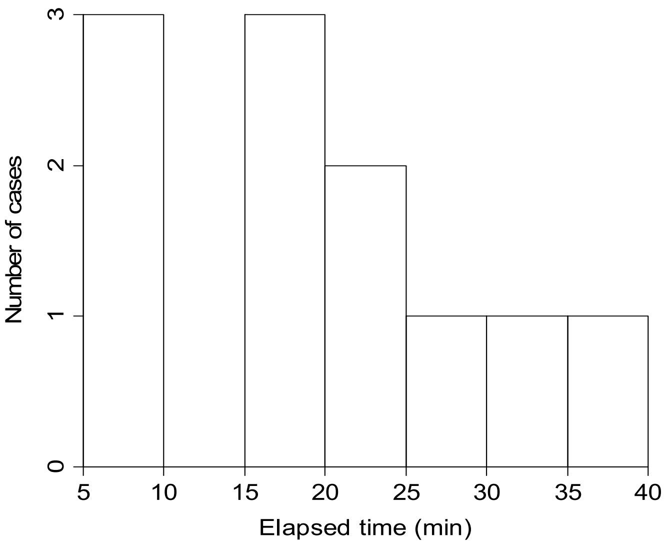

Figure 4. Frequency distribution of elapsed times between the removal of resident male of *Moneuptychia soter* and the new-comer arrival at the focal territory.

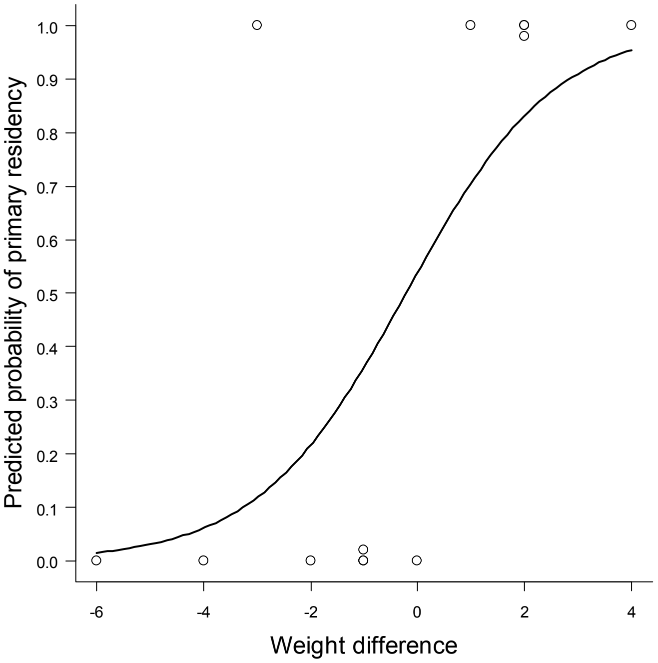

Figure 5. Predicted probability of a male of *Moneuptychia soter* to be in the resident role in relation to the weight difference from its rival. Superimposed points represent different samples with the same focal result and weight.

DISCUSSION

In this study we show that males of the small tropical satyrinae butterflies *H. hermes* and *M. soter* dispute territory through a predictable sequence of agonistic behaviors. Males of *H. hermes* employ a varying sequence of fast circling and ascending spiral flights during disputes, while males of *M. soter* engage in a much slower circling flight that often finish with back and forth linear pursuits accompanied by clicking sounds. Slow motion video did not reveal significant physical contact during the disputes, which suggests that physical fighting is unimportant for contest outcome in these butterflies. Traits associated with physical strength in contest winners may therefore be byproducts of traits that confer contest advantage. In *H. hermes*, the fact that younger males with larger fat reserves (but without higher body or muscle mass) tended to accumulate in the resident role is consistent with the hypothesis that endurance and not physical injury form the basis for desistance by losers in this butterfly. In *M. soter* the interpretation seems more ambiguous, for there is no direct functional link between endurance and male body mass.

Behavioral studies of butterflies point out that disputes typically occur without physical contact (Kemp & Wiklund 2001). However, none of the butterflies known to engage in intense fights (Eff 1962; Pinheiro 2001; Chaves et al. 2006) has received detailed studies. Among the species that have been more carefully investigated, the reduced size associated with the high speed flights during disputes make it difficult to exclude the possibility that physical fighting is occurring. By filming in high speed, we have been able to largely eliminate the possibility that physical fighting occurs in *H. hermes* and *M. soter*. To our knowledge, the only previous behavioral observations using high speed image recording were done for *Pararge aegeria* (Wickman & Wiklund 1983) and *Chrysozephyrus smaragdinus* (Takeuchi & Imafuku 2005). Physical contact was reported in the first species, but not in the second.

If we consider studies for which there was no high speed video recording, the possibility of physical fighting was reported for four butterfly species. However, the traits important to contest resolution are highly variable among them. In *C. smaragdinus*, residents did not differ in the measured morphological or physiological traits from intruder ones (Takeuchi 2006). For the butterflies *Pararge aegeria* and *Hypolimnas bolina*, there are both suggestions that disputes entail (Wickman & Wiklund 1983; Rutowski 1992) and do not entail physical contact (Kemp 2005; Kemp et al. 2006b). In *P. aegeria*, although males may differ in morphology (Shreeve 1987; Van Dyck et al. 1997a; 1997b), victorious males do not seem to differ from losers in any traits linked to flight performance, endurance, maneuverability or physical strength (Kemp et al. 2006a; Kemp et al. 2006b). In *H. bolina*, the most consistent result is that older males have an advantage in winning disputes (Kemp 2001; Kemp 2002b). Finally, *Melanitis leda* also lacks physical contacts, although rivals may sometimes hit vegetation during contests (Kemp 2003). In this species, younger males tended to accumulate as residents (Kemp 2003; Kemp 2005).

Regarding energy reserves, its effect on the territorial success has rarely been investigated in butterflies. Although lipid supply seems to be relevant in resolving the territorial disputes in some odonates (Marden & Waage 1990; Marden & Rollins 1994; Contreras-Garduño et al. 2006) and possibly dipterans (Kemp & Alcock 2003), Kemp et al. (2006b) have recently conceded that butterflies provide little support for the energetic model. In the four butterflies which have been investigated in this regard [*Hypolimnas bolina* (Kemp 2002a; Kemp 2005), *Melanitis leda* (Kemp 2005), *Chrysozephyrus smaragdinus* (Takeuchi 2006) and *Eumaeus toxea* (Martínez-Lendech et al. 2007)] only in *E. toxea* has a significant correlation been found – resident and intruder males had more fat content than did males that won or lost territorial disputes (Martínez-Lendech et al. 2007). Since residents did not differ from intruders in fat content and also winners did not differ from losers, it is improbable that stamina determined by energy supply is important to settle territorial disputes in this species.

Hermeuptychia hermes is the first butterfly species studied to date which consistently shows larger fat reserves in residents than in new-comers. Because the disputes between males do not entail significant physical contact, it is possible that males with higher energetic reserves are able to persist for longer times in an interaction and consequently win contests. On the other hand, it is also possible that energy is not linked to fighting ability, but rather that residents may economize energy by having a territory to perch on. Regarding age effects, *H. hermes* may follow a similar process suggested for *M. leda* (Kemp 2003) and some odonate species (Forsyth & Montgomerie 1987; Tsubaki & Ono 1987). In these species, since age can co-vary with a host of physiological traits, younger males may simply be in better conditions than older rivals. Although resident males of *H. hermes* did not differ from new-comers in FMR or weight, it is possible that other traits not measured in this study vary with age and affect a male fighting ability.

For *M. soter*, the accumulation of heavier males in the resident role remains a puzzle. Although the sample size was small, the weight difference was large and clearly significant. However, since their disputes seemed high ritualized and entirely lacked physical contact, it is difficult to imagine how mass or size may translate into costs and functionally affect the chances of victory. Maybe weight is related to other unmeasured traits such as condition, parasitic load (Marden & Cobb 2004) or even specific aerodynamic designs that increase flight speed and maneuverability (Wickman 1992; Berwaerts & Van Dyck 2004). Males in poor conditions or with higher parasitic load may be unable to fly for longer periods or may accumulate costs at a faster rate during the dispute. Alternatively, males with higher flight speed or maneuverability may be able to impinge more costs on their opponents through aerial maneuvers.

The clicking sound emissions at the end of the dispute between *M. soter* males are also enigmatic. In general, the significance of sound production in butterflies is not well understood (Scott 1968; Møhl & Miller 1976; Kane 1982; Monge-Nájera et al. 1998). It has been suggested to play a role in increasing the chances to escape from predators, in resolving territorial conflicts and in female courtship. Maybe the sounds made by males of *M. soter* function as an honest indicator of a male fighting ability (heavier males may produce louder clicking). The winning male may produces it to express “dominance”, displaying that it is strong enough to continue fighting.

Peixoto & Benson (2008) have shown that among 11 butterfly species in which morphological or physiological differences were sought between territorial and non-territorial males, six showed some size or mass difference. Among the five remaining, two (*H. bolina* and *M. leda*) showed age differences between residents and non-residents. The results for *H. hermes* and *M. soter* sum to 13 species, for which, in 10 species resident males differ from intruders in some important respect possibly related to their ability to dispute or the value they put on territories. However, it is intriguing to note that while models for contest resolution seems to provide good explanations for the disputes in some species such as *H. hermes* (Mesterton-Gibbons et al. 1996), other contests such those observed for *M. soter*, are not well explained.

When modeling male-male agonistic interactions, a series of factors may influence the intensity and the types of behaviors adopted during the fight (Bishop et al. 1978; Parker & Rubenstein 1981; Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist & Leimar 1987; Enquist & Leimar 1990). Nevertheless, all asymmetries and the types of cost accrual tend to be collapsed into just two parameters that reflect the male fighting ability and the value of the disputed resource. In particular, factors that may affect the male investment in a dispute (such as the trade-off between the pay-off of winning a mating site and the mating success achieved with non-territorial alternative tactics) are rarely considered. Knowing those factors may help to understand the fight intensity and consequently the roles of morphological and physiological differences among rivals in resolving conflicts.

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CAPÍTULO 2

The interacting role of previous residency and body mass in the territorial contest of the butterfly *Hermeuptychia hermes* (Lepidoptera: Satyrinae)

The interacting role of previous residency and body mass in the territorial contest of the butterfly *Hermeuptychia hermes* (Lepidoptera: Satyrinae)

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Abstract: When fighting for territories, animal species may use many different structures and behaviors to decide the winner of a contest. This great diversity of the types of disputes has stimulated the development of a series of models designed to understand how these conflicts are ultimately decided. However, to be able to investigate the possible rules used by rivals during the contest, it is fundamental to identify extrinsic and intrinsic factors that influence male fighting ability. Among insect species that compete via aerial interactions, the resident of a territory often wins the majority of the contests. This has led some authors to argue the prior residency may be used as the sole factor responsible to settle a conflict, as a way to increase motivation to fight or as a cue used by rivals to assess relative fighting ability. In this work we experimentally evaluated to influence of previous residency on the contest outcome between males of the small satyrine butterfly *Hermeuptychia hermes* (Fabricius, 1775). By comparing the frequency of resident victories in natural disputes with interactions which both rivals were induced to assume the resident role, we showed that prior residency may interact with body mass in defining the contest outcome. In natural disputes, resident males showed high probabilities of winning a contest, although they were similar to losers in body mass. However, in disputes which both males considered themselves as the resident, heavier males won more interactions. This suggests that residency may be an important component of a male willingness to fight, but that it is not the only factor influencing the settlement of a conflict. Despite the correlation between body mass and territorial success, the weight of neither winners nor losers correlated with fighting time. We conclude that, although body mass may be important in defining the victory chances of a male, a reliable measure of RHP must incorporate other interacting traits (such as age, condition and parasitism) that may define a male fighting ability.

INTRODUCTION

Males of many insect species engage in agonistic interactions for the possession of mating sites (Thornhill & Alcock 1983; Shuster & Wade 2003). When fighting, males may use weapons and specialized behaviors, such as those adapted to grappling or biting in beetles (Eberhard 1987) and crickets (Kelly 2006), or engage in mutual chasing without any apparent physical contacts like seen in butterflies (Takeuchi & Imafuku 2005) and damselflies (Marden & Waage 1990).

The great variation in the behaviors adopted during agonistic interactions has incited the proposition of many different theoretical models aimed to understand possible rules used by rivals to settle a conflict (Maynard Smith 1974; Parker 1974; Maynard Smith & Parker 1976; Bishop et al. 1978; Bishop & Cannings 1978; Parker & Rubenstein 1981; Hammerstein & Parker 1982; Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist & Leimar 1987; Mesterton-Gibbons et al. 1996; Payne 1998). Among species that compete via aerial interactions, the war of attrition model without assessment (WOA-WA - Mesterton-Gibbons et al. 1996), the asymmetric war of attrition model (A-WOA - Hammerstein & Parker 1982) and the sequential assessment model (SAM - Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist & Leimar 1987) seems to predominate in the literature. However, although these models share the same prediction that individuals with higher fighting capacity (also called resource holding potential or RHP - Parker 1974) or that places higher value on the disputed resource should win, they differ in the assumptions related to the ways the opponents use information during contests and how contest develop.

The main dichotomy among these models is related to whether each rival use its own information to settle a contest or whether rivals also assess opponents in judging relative fighting ability (Nuyts 1994). The WOA-WA model assumes that, upon encounter, both adversaries should start a series of displays that do not generate any injury that could affect its persistence ability and remain in the contest until one rival give up (Maynard Smith 1974). There is no mutual evaluation of fighting ability and the individual that is able to persist for longer wins the contest (Mesterton-Gibbons et al. 1996). On the other hand, the models A-WOA and SAM consider that each individual is able to examine the role or RHP of its rival and decide their own investment according to this evaluation (Parker & Rubenstein 1981; Hammerstein & Parker 1982; Enquist & Leimar 1983; Enquist & Leimar 1987). While the A-WOA consider that each individual makes an evaluation of their roles at the beginning of the interaction, the SAM assumes that the information about relative RHP is acquired during the dispute, such as a continuous sampling of the relative fighting ability. However, despite their distinct assumptions, both models predict that the more symmetric the opponents (in terms of role, resource value or fighting ability) the longer will be the disputes (Nuyts 1994).

Although the distinction between A-WOA and SAM is difficult for some species (Kemp et al. 2006), if fighting times and fighting ability are known, one can evaluate if males are able to do mutual evaluation or use self-assessment to decide a winner of a contest (Nuyts 1994; Taylor & Elwood 2003). If there is mutual evaluation, contest duration should be positively related to the loser RHP, but negatively related to the winner fighting ability. On the other hand, if males do not use mutual evaluation, the fight duration should be positively related to both winner and loser RHP. In this sense, although fighting times are relatively easy to measure, to be able to test which kind of evaluation is used during a conflict it is fundamental to discover which male traits best reflect fighting ability or the motivation to win a fight.

In many insect species, territory owners are often observed to win almost all of the contests (Waage 1988; Alcock & Bailey 1997; Kemp & Wiklund 2001). This pattern has led many authors to argue that prior residence may be used as a rule to settle an interaction without prolonged evaluation (Maynard Smith & Parker 1976), serve as a stimulus to increase persistence of the owner (Parker & Rubenstein 1981; Hammerstein & Parker 1982) or, since stronger individuals may accumulate as residents, as an indicator of higher RHP (Parker & Rubenstein

1981; Leimar & Enquist 1984; Enquist & Leimar 1987). However, the great majority of those reports are based on observational studies. If previous residency increases a male's willingness to persist in a fight, this will hide the expression of traits that may determine a male RHP in the absence of a resident advantage. Even powerful, males without territories may avoid great investments in fights for defended sites since it may be more profitable to go to search for other vacated areas (Kemp et al. 2006). In this sense, the investigation of interactions without residency asymmetries is an important way to reveal traits behind male fighting ability and to understand possible rules used to settle an interaction.

Experimental manipulations can be an efficient alternative to evaluate the importance of residency advantage in the aerial territorial conflicts in insects. One way to investigate the role of residency on contest resolution is to compare natural fights in which there is a clear role asymmetry such as resident and intruder, with disputes where both rivals are manipulated to behave as residents (Waage 1988; Alcock & Bailey 1997; Kemp & Wiklund 2004). In these situations, if males follow the unique convention that the resident always wins, the disputes should be won by the newly established resident in the confounded experiments with a similar frequency as the original resident victories in disputes with natural role asymmetries. Alternatively, if residency is a cue used to inform fighting ability, the confounded disputes should be longer than the natural ones, although the individual with greater RHP (often the original resident) is predicted to win the contest. Finally, if residency motivates increased persistence, the longer an intruder is allowed to stay in the possession of a territory, the longer will be its fights with the original resident.

It is well known that male territorial butterflies often manifest a residency advantage in contests (Kemp & Wiklund 2001). The few experimental manipulations done within this group suggest that, although prior residence may exert some effect, stronger individuals accumulate in the resident role (Kemp & Wiklund 2004; Takeuchi 2006). Nevertheless, despite these investigations, suggestions of traits that can be related to male RHP were done for very few species (Peixoto & Benson 2008).

In this study we analyze the rules possibly used to settle the agonistic interactions in the butterfly *Hermeuptychia hermes*. Our objectives are two fold. First, we analyze the effect of prior residence on contest resolution to see if residency is used as a conventional cue to define the winner, motivates increased persistence time or conveys information about relative RHP. Second, by inducing fights that lack residency asymmetries, we investigate the role of morphological traits in resolving territorial conflicts and discuss if they can be assessed by rivals during contests.

METHODS

Study organism

Hermeuptychia hermes is a small dull brown butterfly commonly found along forest edges and in grassy fields in many areas of Latin America. In some places, males defend fixed mating sites between 11:00 and 16:00 h (Peixoto et al. *in prep*). The territories typically occur in small sunny gaps (approximately 5 m diameter) on the forest edge, generally located along the entrances of small trails. Territorial males are easily recognized since they repeatedly fly inside the gaps and periodically engage in territorial interaction with conspecific rivals or fly in direction of other insects that fly nearby. Previous studies revealed that resident males in *H. hermes* are, on average, younger and fatter than replacement males that occupy territories after a resident is removed (Peixoto & Beson *in prep*.).

Study Area

The study was undertaken at approximately 1000 m elevation in the Environmental Protection Zone of the Serra do Japi, a forest fragment located in São Paulo State, Brazil (23°14'S; 46°56'W). This area has approximately 35,400 ha and a mean annual temperature of 15.7 °C. The rainy period occurs from September to March and the dry period from April to August (Pinto 1992). The study area was 150 m in length along a 3 m wide unpaved road inside the reserve. Males of *H. hermes* defended up to seven different territory sites in this area. No additional territories were seen within approximately 500 m of the study population.

Territorial disputes

In order to measure the frequency of victory of resident males against intruders, we observed natural territorial contests on at least five days per month from January 2006 to December 2007. Before observations, we marked as many males as possible, and for at least one day after marking, we repeatedly inspected the defended sites. Whenever we identified a contest, we observed the pair until both adversaries stopped interacting and then identified the winner as the male that returned and resumed the territory defense. We only considered as a valid observation, disputes that possessed marked males that defended a territory during the days before the observation or, when this information was not available, for at least 30 min before the start of the interaction. After we identified both the winner and loser males, we captured them to carry out body mass and wing wear measurements.

To measure fresh body mass in the field, we transferred each butterfly (still alive) to a small pre-weighed envelope and weighed the individual on a portable balance (Pocket-Pro model PP-2060D, sensitivity 1 mg). We also visually estimated wing wear on a scale of 0-2 that was used as a measure of butterfly age. We scored individuals with soft wings and no scale loss as young (0), with hard wings and little scale loss as intermediate (1) and with hard wings and much scale loss as old (2). The usage of wing wear as an index of age has been widely used in butterfly studies (Kemp 2000; Conradt et al. 2002; Kemp 2005).

Removal-replacement experiment

In order to evaluate the effect of prior residency in resolving territorial conflicts, we carried out an experiment in which two rivals were induced to consider themselves territorial owners (induced fights) from February 2007 to April 2008. To perform this experiment, we observed the behavior of marked males for at least one day after marking to ensure that it was the owner of a territory. After identifying the resident male, we removed and placed it in a partially isolated thermal box (polystyrene foam; base: 15.5 x 15.5 cm; height: 18 cm) located in sunny areas. Boxes were left in sun because in a pilot study in which boxes were placed in the shadow, none of the 10 resident males tested returned to reclaim its territory.

After the resident removal, we waited until the territory was occupied by an intruder that was allowed to occupy the vacated site for at least 1800 s before releasing the original resident. However, after being freed, the original residents often spent several minutes inside the forest before returning to the territory. Consequently, intruder males frequently stayed for more than 1800 s in the possession of the focal site.

After releasing, we observed the behavior of both males inside the focal territory and when a territorial dispute started, we timed the interaction until one male had won. At the end of each observation, we captured both winner and loser to carry out body mass and wing wear measurements following the procedures described in previous topic. Afterwards, we placed those individuals in an ice-filled box and transferred them to laboratory to perform fat and muscle extractions.

Fat and muscle mass extractions

To estimate fat content, we dried males in a drying oven (at 70 ^{o}C) for 96 h. Next, we separately weighted the thorax (without wings and legs) and abdomen of each individual in a Can C-30 Microbalance (precision 10^{-5} mg). After weighing, we placed all body parts of each butterfly in a closed vial containing 5 ml chloroform for 48 h to extract lipids. At the end of the extraction period, we returned the fatless body parts to a drying oven for additional 96 h and later re-weighted them. We calculated fat content as the weight difference before and after immersion in chloroform (Plaistow & Siva-Jothy 1999). This technique has been previously tested for this species and has shown itself efficient in extracting body lipids (Peixoto & Benson, *in prep.*) We calculated muscle mass in the same way. However, we immersed only the male thorax in 10 ml of 0.35 M sodium hydroxide for 72 h (Marden 1987). We estimated the muscle mass as the difference in the fatless thorax mass minus muscle extracted thorax mass.

In order to obtain measures of fat content independent of male size, we used the standardized residuals of a linear regression between fat content as the dependent variable and fatless body mass as the predictor variable. For size independent values of flight muscles, we used the standardized residuals from a linear regression between thoracic muscle mass and total dry body mass. This value (also called flight muscle ratio or FMR) is frequently used as an estimator of the maneuverability capacity during aerial interactions in insects (Marden & Chai 1991; Marden & Rollins 1994; Contreras-Garduño et al. 2008).

Statistical analyses

Frequency of victory

To investigate the influence of resident-intruder asymmetries on contest resolution, we compared the frequency of the original resident victory in natural and induced fights using a chi-square test (Zar 1996). We considered the role of the winner male (resident or intruder) as the response variable and the type of dispute (induced or natural) as the predictor variable.

Effect of male traits on contest outcome

For both the removal-replacement experiments and natural fights, we used a logistic regression to analyze the influence of male traits on the chances of victory (Hosmer & Lemeshow 1989). However, since these disputes represent paired events, we randomly chose half the interactions to assign a focal condition to the winner male (condition 1) and to the loser male on the other half (condition 0). For each pair, we calculated the difference for each trait as the value of the focal individual subtracted from the value recorded for its non-focal rival. This procedure allowed the use of each pair as a sample unity to evaluate the chances of victory of the focal male in relation to the traits differences from its rival.

For the removal-replacement experiment, since there was more than one predictor variable, we used an information theoretic approach to select the most parsimonious logistic model describing the chances of victory by a focal male. We tested the fit of models with different combinations of the predictor variables (interaction terms were not used) and selected the candidate model with the smaller bias-corrected value for small samples of the Akaike information criterion as the best candidate (Burnham & Anderson 2002). We performed all statistical analyses using the R software (R Development Core Team 2004).

Removal-replacement experiment and fight duration

To evaluate if males are able to perform mutual evaluation during disputes or if disputes are resolved based on self-assessment, we compared the dispute duration with winner and loser traits (Taylor & Elwood 2003). For the relationship between fight duration with fresh mass and residual fat content of loser and winner males, we used a ranged major axis regression (Legendre & Legendre 1998; Legendre 2001) because both response and predictor variables represented random factors (Quinn & Keough 2002). For the relationship between fight duration and wing wear of rivals, we used two one-way analyses of variance (one for winner and other for the loser males). For all analyzes, we considered the interaction duration as the response variable and characters related to RHP of the loser and the winner males as the predictor variables. Measures of fight duration were log transformed to meet test assumptions. For the ranged major axis regression, p values regarding the significance of the estimated slope were calculated based 500 permutations of the response variable (Legendre 2001).

To investigate the influence of residency time on the dispute duration, we compared the time the intruder male spent in the possession of the territory with the interaction duration using a major axis regression (Legendre 2001). We considered the fight duration as the response variable and the residency time as the predictor variable. Data on both variables were log transformed to improve the homogeneity of variances.

RESULTS

We observed 34 natural disputes which we could clearly identify a winner (and a loser) male. Both rivals were captured and the complete interaction timed in 23 of them. Among these, five interactions lasted for less than 4 s and consequently may not represent true contests (Peixoto & Benson, *in prep*.). Among the 18 remaining observations, eight interactions involved four males that disputed twice against different rivals, resulting in 14 independent observations. In four interactions (two involving the same male against different rivals), a heavier intruder male dislodged the resident after lengthy disputes that lasted on average 1581 (min-max=82-5904) s. The mean fight duration in the other 14 fights which did not have resident turn over (counting the partially dependent interactions) was 17 (min-max=5-37) s.

In the experiments in which both adversaries played the resident role, we conducted a total of 104 trials. Among these, 29 represented disputes where the original resident male contested his previous territory with an intruder male. We successfully re-captured resident and intruder males after 18 of these conflicts and timed the complete interaction in 16 situations.

However, we simultaneously captured both rivals and timed the complete interactions for 13 pairs. The unsuccessful trials represented cases in which the territory was not occupied by an intruder male (34 cases), the resident did not return to the territory (29 cases) or overcast conditions (7 cases). In another trials, the intruder occupied the territory, but abandoned the area before releasing the original resident (2 cases), winner and loser males mixed up in which resident status was ambiguous after fighting (2 cases) and fight was interrupted by people in the study area (1 case). The induced fights averaged for 123 (min-max=4-720) s, which was 7.3 times longer than the time spent by males in natural fights without resident dislodgement (t test for separate variances estimates, $t=2.58$, $df=15$, $p=0.021$).

Frequency of victory

Since we are concerned with the frequency of primary resident victory in natural vs. induced fights irrespective of morphological or physiological differences among rivals, we used all data corresponding to the 34 natural fights and the 29 experimental trials which we could identify a winner and a loser male. In the natural disputes the resident won more fights when compared to the frequency of victory of the original resident in the removal-replacement experiment ($\chi^2=5.40$, $df=1$, $p=0.020$). The resident male won 27 (79%) of the 34 natural disputes and 15 (52%) of the 29 induced conflicts. If we restrict our analysis to the independent or partially dependent contests that lasted for more than four seconds and for which we captured both rivals after the interaction (19 natural and 17 induced disputes), the frequency of resident victory becomes similar among natural (78%) and induced (59%) conflicts ($\chi^2=1.71$, $df=1$, $p=0.191$).

Effect of male traits on contest outcome

The logistic model with all predictors variables did not reveal any relationship between male traits and the chances of winning ($AIC_c=32.2$, $n=18$, $\chi^2=7.71$, $df=4$, $p=0.102$). However, the most parsimonious candidate model included only fresh mass as the predictor variable (AIC_c=24.4). This model indicated that heavier males tended to win contests when the residency role was confounded (χ^2=5.34, df=1, p=0.021, Fig.1). Models including only age (AIC_c=28.5) or residual fat content (AIC_c=28.6) did not indicate differences between winners and losers (χ^2=1.29, df=1, p=0.256; χ^2=1.15, df=1, p=0.284 for age and residual fat content respectively). In natural disputes, male weight did not affect the chances of winning (χ^2=0.18, n=23, df=1, p=0.672). This relationship did not change after discarding the five disputes that lasted for less then four seconds (χ^2=1.66, n=18, df=1, p=0.198).

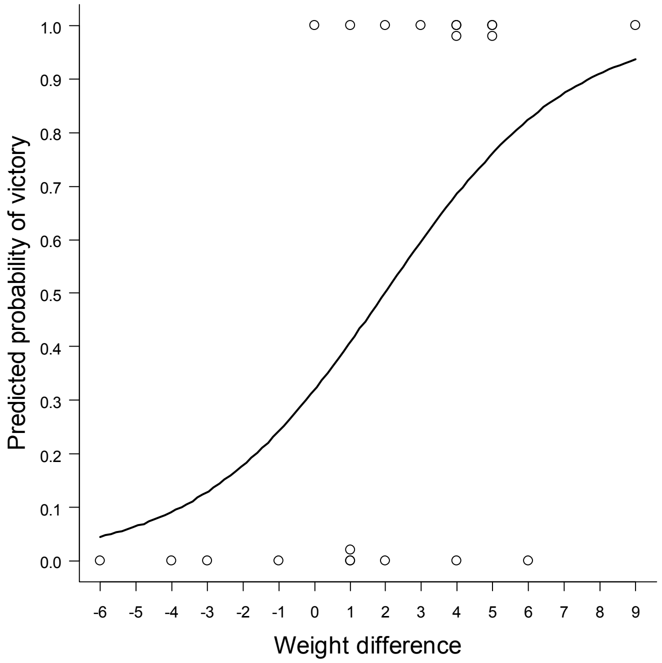

Figure 1. Predicted probability of victory of focal males of *Hermeuptychia hermes* in relation to the weight difference from its rival after fighting in the removal-replacement experiments. Superimposed points represent different samples with the same focal result and weight.

Removal-replacement experiment and fight duration

Among the 13 timed fights, one lasted for four seconds. Since this observation is an outlier and may not represent an actual contest between males, we removed it to perform the statistical procedures. However, no qualitative alterations in the results occurred because of its removal.

In the removal-replacement experiments, all winner males were either young or intermediate individuals. The fight duration was unrelated to either winner ($F_{(1,10)}$=0.96, p=0.349) or loser ($F_{(2,9)}$=0.52, p=0.609) wing wear. Similarly, there was no relationship between fight duration and fresh body mass or residual fat content (Table 1, Fig. 2). For the analyses using male body mass, we excluded a pair of extremely light individuals (16 and 18 mg for winner and loser males respectively) that stood as outliers in both regressions (Legendre 2001). Among the natural disputes that lasted for more than four seconds (n=14), loser (b= -14.27; p=0.158) fresh body mass were unrelated to fight duration, while winner males tended to have longer contests when they were small (b= -12.53; p=0.07). In order to meet the test assumptions, we did not include in this analysis the four interactions in which the intruder male won. These were very long interactions that appeared as extreme outliers when compared to natural disputes in which resident males won.

Table 1. Ranged major axis regressions between fight duration and winner and loser traits in the removal-replacement experiments. Values of b were back-transformed to represent the original log transformed data (Legendre 2001).

Trait	Position	b	p	Corresponding graph in Fig. 2
Body weight (mg)	Winner	-1.49	0.386	A
	Loser	0.37	0.364	B
Residual fat content (mg)	Winner	-0.55	0.132	C
	Loser	-0.16	0.316	D

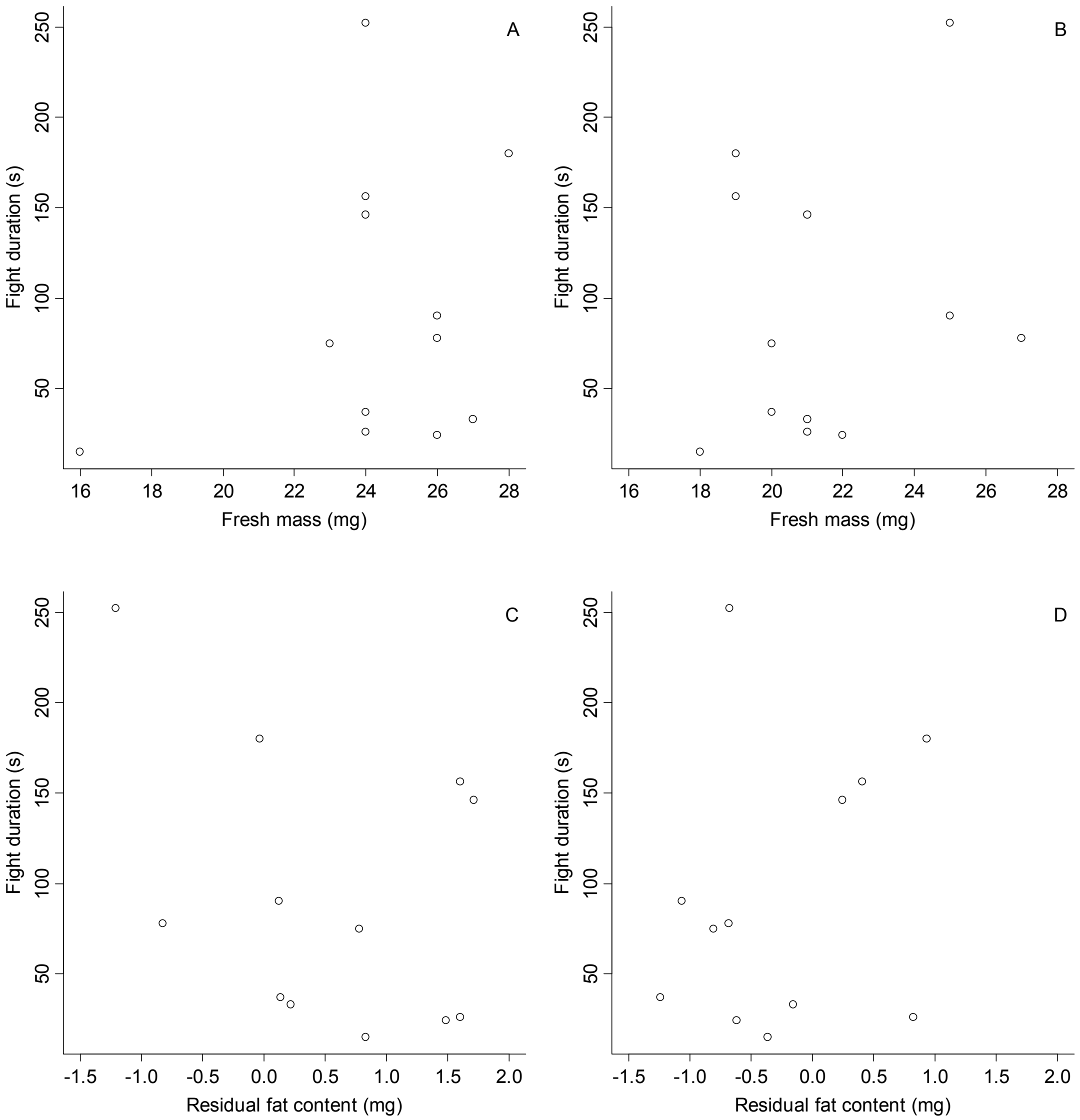

Figure 2. Fighting times in relation to the fresh body mass and residual fat content of winner (A and C) and loser (B and D) males.

Intruder males were allowed to defend the focal territories for a mean of 2635 s (sd=1010, n=13) before the original resident return to contest his previous territory. However, intruders that held a territory for more time did not participate in longer interactions (b=32.03; p=0.398). Although these data had an outlier represented by an intruder male that defended the territory for approximately 5880 s but fought for just 90 s, its removal from analyzes did not notably alter the results (b=33.63; p=0.200).

DISCUSSION

In this study we show that males of *H. hermes* may use residency asymmetries to settle territorial conflicts, although in the small fraction of natural contests won by intruders, large size appear to be decisive. In addition, the fact that heavier males seem to have a winning advantage in the removal-replacement experiments, shows that traits other than residency status also play an important role in settling territorial conflicts. Intruder males did not increase their fighting times when allowed to defend the focal site for longer periods, but incurred greater chances to win a contest if residency status was confounded. Although our results suggested that weight is potentially related to male RHP, there was no relationship between fight duration and winner or loser body mass. However, the tendency of lengthening of contest duration with smaller winners in natural fights may indicate that large sample sizes could alter this conclusion.

Among insects, there are just a few experimental manipulations designed to test the effect of previous residency on contest resolution. All, with one exception (Davies 1978), suggest that residency does not act alone in affecting the chances of winning. In the wasp *Hemipepsis ustulata* (Alcock & Bailey 1997) and the butterflies *Pararge aegeria* (Kemp & Wiklund 2004) and *Chrysozephyrus samaragdinus* (Takeuchi 2006), experiments that inverted the resident role, show that, although disputes lasted longer when both individuals considered themselves as the territory owners, original residents had a greater chance to win an interaction. In the damselfly

Calopteryx maculata, males without territories can sometimes naturally occupy the defended sites when the original resident is away. However, these newly established males also had fewer chances to win contests when the primary residents returned to reclaim their previously defended sites (Waage 1988).

The original resident advantage gives strong support for the hypothesis that individuals with higher RHP accumulate on territories in the resident role (Leimar & Enquist 1984). However, traits related to fighting ability are not easily identified. For *P. aegeria* and *C. smaragdinus*, no morphological or physiological traits that could be functionally related to greater fighting ability were detected. In *H. ustulata*, body size (indicated by head width) seems to be the sole factor that consistently differed between winners and losers.

Our results with *H. hermes* are similar to those described above in the sense that, when both adversaries were induced to behave as residents, the fights were longer than the natural conflicts. However, in *H. hermes* it seems that the original resident advantage at winning the territorial interactions is dependent on whether there is role related asymmetry: when there was confusion about residency, body mass became important at defining the winner, but when there was role asymmetry, residents held the greater chances of victory. Maybe, as was described for the wasp *H. ustulata* (Alcock & Bailey 1997; Kemp et al. 2006), contests with role asymmetry rarely represent conflicts in which intruder males invest greatly in fighting. Although the ability for mutual evaluation seems to be rare among insects (Kelly 2006; Kemp et al. 2006; Briffa 2008), if stronger or more motivated males accumulate on territories, intruder males that are able to assess the residency role, may avoid wasting time and energy in disputes that have higher chances to be very long and costly (Enquist & Leimar 1983; Leimar & Enquist 1984). The results in the removal-replacement experiments suggest that stronger males of *H. hermes* do not accumulate in the resident role, but resident males clearly invest more in fighting. In this sense, when there is residency asymmetry, intruder males must be less willingness to invest heavily in fights. Consequently, some traits important to contest resolution may be “masked” by the residency asymmetry in natural fights, but revealed when both males were induced to behave as residents (Kemp et al. 2006).

Stress possibilities can also influence our results. It may be that the original residents were stressed while they were kept in the thermal boxes in ways that affected their subsequent willingness or ability to fight. Although we can not completely exclude the stress possibility, we think that it is improbable since original residents fought for periods that were well within the time range registered for natural fights with residency turn over. If stress was an important factor, disputes lost by resident males should have been relatively short.

The experiments on fight duration and RHP did not indicate either mutual or self-assessment as tactics employed during a contest, which contrast with other results for insects (Marden & Waage 1990; Marden & Rollins 1994; Kelly 2006; Kemp et al. 2006; Briffa 2008). For the terrestrial species in which injury constitute a contest cost, rivals seems to base their decision to remain or retreat according to their own capacity to sustain damage (Kelly 2006; Briffa 2008). In species that compete via aerial interactions, there is evidence for both self-assessment of persistence capacity (Marden & Waage 1990) and mutual evaluation of fighting ability (Kemp et al. 2006).

Due to the small sample size for interaction times, our results about self or mutual evaluation in *H. hermes* must be interpreted with caution. If our data are representative, the absence of a relationship between fight duration and RHP may indicate that fresh mass is not the only factor responsible for contest resolution. As suggested for *H. ustulata* (Kemp et al. 2006), a male’s fighting ability may be determined by numerous factors that may interact to define his RHP. In support of this, an earlier investigation of asymmetries between resident and non-resident males of *H. hermes* suggested that age and fat content may also play a role in resolving the territorial conflicts in this species (Peixoto & Benson, *in prep*.). In addition, other unmeasured traits, such as condition and parasitism, are important determinants of the fighting ability in other flying insect species (Córdoba-Aguilar & Cordero-Rivera 2005; Contreras-Garduño et al. 2006; Contreras-Garduño et al. 2008) and, thus, may be important for *H. hermes* as well.

On the other hand, if fights actually last longer when the winner is smaller, this may indicate that some kind of evaluation is being performed during the dispute, since in the case of self-evaluation this relationship should be positive (Taylor & Elwood 2003). For *H. hermes*, our results may indicate that, although losers seems to evaluate the fighting capacity of winners, the opposite is not true. Since this pattern occurred in natural fights, this means that intruders may evaluate residents, but residents do not evaluate intruders. Maybe the motivation of resident males to maintain their territories is high enough to compensate for strong investments in fights without necessity of evaluating the fighting ability of its rival. The opposite pattern of residents evaluating intruders is improbable because small residents should, on average, meet larger rivals. Consequently, the lighter the residents, the smaller should be their investment in interactions (Parker & Rubenstein 1981; Hammerstein & Parker 1982; Enquist & Leimar 1983), generating a positive relationship between RHP and fight duration for winners.

Male *H. hermes* provide a clear example of how fighting may depend on a series of factors that will ultimately influence how each individual must invest in a dispute. It is interesting to note that prior residency may play a key role in studies involving RHP asymmetries. Consequently, if one wishes to discover morphological or physiological traits related to fighting ability, residency effects must be accounted for. In addition, the lack of adequacy between the fighting behaviors of *H. hermes* and the models predictions about self or mutual evaluation of fighting ability suggest that measures of RHP may be sometimes equivocated. Alternatively, it may also indicate the need of improvements in the fighting rules postulated by those models.

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CAPÍTULO 3

The presence of feeding resources determining the adoption of resource defense polygyny as an alternative mate-locating tactic in a lekking butterfly

The presence of feeding resources determining the adoption of resource defense polygyny as an alternative mate-locating tactic in a lekking butterfly

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Abstract: Among polygynous species, defense-based male strategies to encounter sexually receptive females can be divided into three major groups: the direct defense of females (female defense polygyny), defense of resources used by females (resource defense polygyny) or defense of specific sites that lack resources, but are consistently visited by sexually receptive females (lek). Although males in the same population generally tend to adopt a single reproductive behavior, competition may force some individuals to adopt alternative mate-locating tactics. It is very common for weaker males to adopt non-territorial tactics, although in a few cases the adoption of alternative territorial strategies may also occur. However, since the usage of alternative territorial tactics seems relatively uncommon in arthropods, the knowledge of the factors that drive its adoption is limited. In this study we investigate the adoption of a resource based territoriality as an alternative to a non-resource based one by males of the butterfly *Paryphthimoides phronius* (Buttler, 1867). Male *P. phronius* are commonly found defending sunny patches lacking evident resources in the forest edge (a system that can be regarded as non-resource base territoriality). However, after inserting fermenting fruit in previously undefended sites, we showed that males may also adopt a resource defense tactic. Although males located on territories with decomposing fruits were heavier than males on the sunny clearings, preference experiments showed that the defense of sites without resources seems to be preferred by males. The patterns described here indicate that more than one mating system may occur in the same population and that ecological factors (such as the spatial distribution of feeding resources) may play an overriding role in this variation. Although this is the first experimental investigation of this flexibility in butterflies, we argue that a more comprehensive investigation of the ability to change from a resource to a non-resource based system inside the subfamily Satyrinae can turn it an excellent candidate model to test the evolution of different territorial mating organizations.

INTRODUCTION

Mating systems which males fight among themselves for access to females or mating territories are very common (Thornhill & Alcock 1983; Shuster & Wade 2003). Although there is a great variation in the proposed classifications of these systems (Thornhill & Alcock 1983; Shuster & Wade 2003), the tactics adopted by males to increase mating success may be used to define three major groups: female defense polygyny, resource defense polygyny and leks (Emlen & Oring 1977; Höglund & Alatalo 1995). In female defense polygyny, males directly defend groupings of females (harems) from other males. In resource defense polygyny, males defend resources important to females (such as feeding or ovipositing sites) and try to copulate with sexual partners that arrive to use those resources. Finally, at leks males defend territories or small arenas at specific landmarks. Since those sites do not contain any resources suitable to female use, they often visit such places just to copulate and leave after being fertilized.

It is usual to have more sexually receptive males than available territories or females (Alcock et al. 1978; Kemp & Wiklund 2001). Consequently, males commonly have to fight for the possession of these limited resources. In this context, the conquest and maintenance of a territory require that a new arriving male win the site through a contest with the current owner and maintain ownership through contests with subsequent challengers. Since weaker males are frequently excluded from territories, the adoption of alternative mating tactics by those individuals may be the only option to acquire sexual partners (Andersson 1994; Alcock 1997).

Many arthropod species have evolved a series of alternative mating tactics. The most typical examples are species in which males show two morphs with one being strongly territorial and the other attempting sneaky copulations at the defended sites without being noted by the territory owner (Emlen 1997; Buzatto & Machado 2008). In other situations, males may be very similar morphologically, but with individuals in poor condition adopting alternative mating tactics that often yield fewer copulations than the territorial one (Wickman 1985; Forsyth &

Montgomerie 1987; Bergman et al. 2007). Those alternative tactics may vary from non-territorial patrolling through the defense of alternative low quality areas, which determine in some cases, the existence of more than one mating system in the same population (Yeates & Dodson 1990; Alcock 1994; Groddeck et al. 2004).

Despite the commonness of alternative reproductive behaviors in arthropods, the evolution of different mating systems and strategies is still much debated (Thornhill & Alcock 1983; Andersson 1994; Höglund & Alatalo 1995; Shuster & Wade 2003). In particular, it is not well understood how the use of mating sites without resources may have evolved. It is possible that, when the probability of encounter between sexes is low, males and females that use some specific landmark point (such as hilltops) enjoy higher reproductive success and consequently evolve territorial strategies not related to the presence of resources (Höglund & Alatalo 1995). Alternatively, it may be that a non-resource based territorial system may have originated from a resource-based one (Parker 1978). In this context, the comprehension of how males adopt alternative mating tactics, and in particular, the identification of species which males may use both resource based and non-resource based territoriality, may be an important step to understand the processes leading to the evolution of different territorial mating organizations.

Butterflies are good organisms for the study of mating systems because they are a relatively well known group with a wide variety of mating strategies (Rutowski 1991; Wickman 1992). Many species present leks, in which males may occupy territories that vary from small sunspots to large topological features such as hilltops. Yet, other species defend flight corridors (Alcock 1994), specific plant species (Alcock & Gwynne 1988; Rutowski 1992) or female pupae (Brown 1981). Oviposition or feeding resource defense systems are rare in this group. Males of a few species defend areas with larvae host plant (Rutowski 1991; Lederhouse et al. 1992), aggregations of non-host plants that present nectar producing flowers (Suzuki 1976; Fischer & Fiedler 2001) and one possible case of areas with fermented soft fruits (Moore 1999). Among the territorial species, the most commonly reported alternative mating tactic is patrolling behavior in which males fly over more or less extensive areas in search of sexually receptive females (Wickman 1985; Alcock 1994; Merckx & Van Dyck 2005).

Males of the butterfly *Paryphthymoides phronius* (Nymphalidae: Satyrinae) typically defend territories in sunny clearings (from now on called sunspots) without evident resources as the main mating tactic (a mating system that can be regarded as a dispersed lek - Alcock 1981). Lighter males, which seem less able to defend such sunspots, apparently wander in the vicinity of territories and occupy them in the absence of owners (Peixoto & Benson 2008). However, field observations indicated that male *P. phronius* may adopt a third tactic by defend temporary territory sites associated with decomposing fruits. Since males and females of *P. phronius* feed on decaying fruits (Peixoto & Benson 2009), this third tactic possibly constitutes an additional alternative system based on resource defense.

Although there is a suggestion of the existence of a resource based and a non-resource based territorial mating system for butterflies (Moore 1999), to our knowledge this possibility has never been experimentally evaluated. In this study we developed a series of experimental manipulations to investigate the ability and preference of males to change between these two reproductive behaviors. Since in a lekking system only receptive females visit the mating territories (Alcock 1981), while in a resource defense system, females may visit the defended sites in order to benefit from resources and not specifically to mate (Groddeck et al. 2004), our main expectation was that territories with resources are less valuable. Consequently, the defense of sunspots without evident resources should be preferred and adopted by individuals in higher condition.

METHODS

Study site

We conducted experiments along a strip of 2.7 km forest edge at the Santa Genebra Municipal Reserve (Campinas, SP, Brazil; 22°50'S, 47°06'W). The reserve is a disturbed fragment of deciduous Atlantic forest with area of ca 250 ha. The climate is subtropical with a cool dry season from May to September and a warm wet season from November to March. Mean annual rainfall is 1,360 mm and mean annual temperature is 20.6 ºC.

Resource defense experiment

To evaluate if males can be induced to establish territories by the presence of decomposing fruits, we selected 24 undefended sunspots along the border of the reserve during March and April 2007. To ensure that these sites were not occupied by territorial males, we inspected them between 11:00 and 14:00 h (period in which males typically begin to defend territories - Peixoto & Benson 2009) on the two days before starting the induction.

After the inspection on the second day, we placed fruit resource consisting of a banana that had been fermented in sugar cane juice for at least 48 h on half the sunspots (randomly selected). During the following two days we inspected the sunspots with and without the resource for the presence of territorial males. Whenever we found a male in the experimental sunspots, we observed it for at least one minute to ensure that it was defending the focal site and immediately netted it to measure body mass, wing area and fat content independent of male size (also called residual fat content - see below for a detailed description). Territorial males were easily recognized because they repeatedly perched in the same small area and flew up to nearby flying insects. They also did not abandon their territory when we walked inside the area. For each male captured on an experimental sunspot, we tried to capture a territorial male from a traditionally defended site that do not present feeding resources. After a period of one week, we repeated the procedure with the sunspots that received fermenting banana inverted. In this second series, if an experimental territory from the first replication was still being defended by a territorial male, we excluded it from analyses. All observations were made on sunny days.

We correlated the presence of territorial males with the presence of resources using multiple logistic regression (Hosmer & Lemeshow 1989). We considered the presence of a territorial male as the response variable and the presence of fermenting fruit and trial sequence as predictor variables. To select the most parsimonious model describing the probability of a male defend a site in relation to the presence of fermenting fruit, we used an information theoretic approach (Burnham & Anderson 2002). The model that presented the smaller value of the bias-corrected version of the Akaike information criterion (AIC_c) was selected as the best candidate (the interaction between presence of bait and trial sequence was included in the analysis).

To test for body mass, residual fat content and wing area differences between males from the traditional and resource induced territories we used a multiple logistic regression (Hosmer & Lemeshow 1989). We considered the tactic (defense of resource-based or traditional territory) as the dependent variable, and body mass, wing area and residual fat content as independent variables (interaction terms not included). To identify the most relevant variables for the relation between the probability of a male occupy a resource supplied or a traditional site in response to their morphometrical and physiological characteristics, we used the bias corrected version of the Akaike information criterion as described above. We used the R software (R Development Core Team 2004) to perform all statistical analyses.

Resource access experiment

To evaluate if the availability of fermenting fruit for feeding can increase a territorial male body mass, we conducted a second experiment using 22 sunspots along the reserve border between October and December of 2007. Again, before the beginning of the experiment, we inspected all sunspots for two consecutive days to ensure that no site was defended by a territorial male. After inspection on the second day, we placed a fermenting banana with sugar cane juice bait in the sunspots, but covered the bait with a hemi-spherical exclusion cage (20 cm diameter plastic food strainer; 0.5 mm mesh) in half the sites (randomly chosen). These exclusion cages allowed the release of the resource odor, but prevented feeding by butterflies (Fig. 1).

Figure 1. Exclusion cage used to prevent the feeding of the fermenting fruit placed inside the experimental sunspots.

After placing the baits, we inspected the sunspots on the following two days for territorial males. Whenever we found a male defending an experimental sunspot, we captured it to perform body mass and residual fat content measurements (see below). Due to bait removal by vertebrates in some sites without exclusion cages, we added a small portion of fermenting fruit in the morning of the second day (08:00 – 09:00 h).

We tested for differences in traits between males that were allowed and not allowed to feed on the fermenting fruit using t tests (Quinn & Keough 2002). We considered body mass and residual fat content as dependent variables and the access to the bait as the predictor variable.

Body mass, wing area and fat content estimations

For body mass measurements, we transferred each male as soon as captured to a small pre-weighted envelope and weighed it on a portable balance (Pocket-Pro® model PP-2060D, sensitivity 1 mg). To estimate wing area, we photographed the individuals with a digital camera and measured the wing area using the software ImageJ v1.37. We measured only one wing per male.

To estimate fat content, we dried butterflies in an oven (at 70 °C) for 96 h. Next, we separately weighted the thorax (without wings and legs) and abdomen of each individual in a Can C-30 microbalance (precision 10^{-5} mg). After weighing, we placed all body parts in a closed vial containing 5 ml chloroform for 48 h to extract lipids. Afterwards, we returned the fatless body parts to a drying oven for additional 96 h and re-weighted them. This technique proved effective in removing all fat in a related species (Peixoto & Benson, *in prep.*). We calculated fat content as the weight difference before and after extraction in chloroform (Plaistow & Siva-Jothy 1999). In order to obtain measures of fat content independent of male size (residual fat content), we used the standardized residuals of a linear regression between fat content as the dependent variable and fatless body mass as the predictor variable. For each experiment (resource defense and resource access), we pooled males from the two treatments in order to perform the linear regressions.

Preference experiment

To evaluate if males prefer the traditional territories without resources or the sites containing fermenting fruit, we conducted an additional experiment between January and April 2008. Using a permanent ink pen, we marked all males seen defending traditional territories along the border of the reserve (focal males). After resighting a marked male in a territory for at least one day after marking, we selected two undefended sunspots in a 5 m radius from that territory and placed fermenting banana bait in both. On the following morning we added little more banana (between 08:00 and 08:30 h) to compensate loss to vertebrates.

On the day after settling out the bananas, we visited the territories between 12:00 and 14:00 h to check if the marked males remained in their territories or had transferred to the vicinity of a fruit resource. During this inspection, if we saw an unmarked male defending the experimental sites we removed it in order to guarantee the focal male free access to the resource. To test if males prefer traditional sites or territories with fermenting fruit, we conducted a chi-square test. We compared the presence of males in each site against an expected null distribution if males had 50% of chance to switch to the experimental sites (Quinn & Keough 2002).

RESULTS

Resource defense experiment

The complete model describing the effect of resource (fermenting banana) and trial sequence on inducing territory establishment in *P. phronius* indicated that the arrival of territorial males responded to both presence of fermenting fruit and trial (AIC_c=46.4, χ^2=20.02, p<0.001). However, the most parsimonious candidate indicated that only the presence of fermenting fruit was important in attracting territorial males (AIC_c=43, χ^2=19.48, p<0.001). In the first repetition 11 out of 12 (91.7%) sunspots that received fermenting fruit were defended by a territorial male for at least one day, while only one sunspot which did not receive fruit was defended in the same period. In the second trial, five sites had territorial males presented at the start of the experiment and were excluded from the analysis. The pattern obtained for the remaining 19 sunspots was very similar to that observed in the first repetition. Eight out of ten (80%) sites that received decomposing fruit were defended, while only one of nine (11.1%) without bait was occupied by a territorial male.

We captured 20 territorial males from territories that received fruits and 18 others residents at typical non-resource sites. Although the model including only body mass was almost as good as the most parsimonious model, the model that minimized the bias corrected version of the Akaike information criterion included body mass and wing area (Tables 1 and 2). Although no male was observed feeding on the fermenting fruit, the residents from territories with resources were 10% heavier than males from the traditional ones (Fig. 2). However, despite the most parsimonious model included wing area as important in the distinction between the two categories of males, we found only a slight tendency with males at non-resource territories having larger wings (Fig. 3).

Table 1. Summary of logistic models describing the probability of a male of *Paryphthimoides phronius* occupying a territory containing fermenting fruit in relation to a territory without fruit. The models were ranked in ascending order of their AIC$_c$ values (**Δ_i** represent the difference between the AIC$_c$ of model i and the AIC$_c$ of the most parsimonious model; w_i is the Akaike weight of model i).

Model	**AIC$_c$**	**Δ_i**	**w_i**	**Df**	**χ^2**	**P**
Body mass + wing area	49.845	0.000	0.360	2	9.40	0.009
Body mass	49.878	0.033	0.354	1	7.02	0.008
Residual fat content + body mass + wing area	51.759	1.914	0.138	3	9.96	0.019
Residual fat content + body mass	52.050	2.205	0.120	2	7.19	0.027
Wing area	56.451	6.606	0.013	1	0.45	0.504
Residual fat content	56.874	7.029	0.011	1	0.02	0.877
Residual fat content + wing area	58.715	8.870	0.004	2	0.53	0.769

Table 2. Mean values of body mass, wing area and residual fat content of males of *Paryphthimoides phronius* collected in the resource defense experiment and resource access experiment. Values in parentheses show the standard deviation of the observations.

Trait	Resource defense experiment		Resource access experiment	
	Traditional site males	**Resource induced males**	**Access denied**	**Access permitted**
Body mass (mg)	23.11 (1.32)	25.40 (3.57)	22.85 (2.56)	25.06 (3.49)
Wing area (mm^2)	22.0 (1.8)	21.6 (2.1)	-	-
Residual fat content (mg)	0.03 (1.14)	-0.02 (0.85)	-0.19 (0.84)	0.20 (1.11)

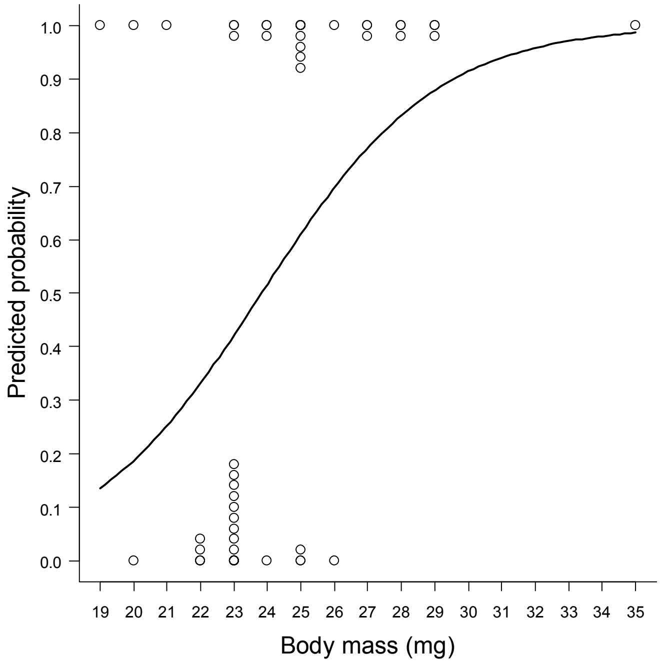

Figure 2. Predicted probability of a male *Paryphthimoides phronius* defending a territory containing fermenting fruit (1) or traditional sites that never received resources (0) in relation to its body mass. Superimposed points represent different males with the same tactic and body mass.

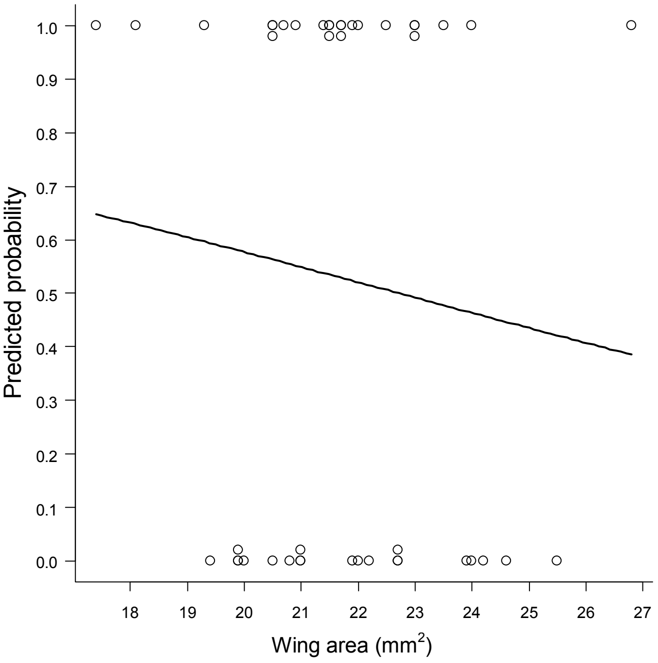

Figure 3. Predicted probability of a male *Paryphthimoides phronius* defending a territory containing fermenting fruit (1) or traditional sites that never received the resources (0) in relation to its wing area. Superimposed points represent different males with the same tactic and body mass.

Resource access experiment

We collected 17 males from the territories with free access to the fermenting fruit and 20 from the territories with exclusion cages. Males from the free access territories were 9.1% heavier than males which could not feed on the bait (t=2.22; df=35; p=0.03; Table 2). We quantified the residual fat content of 16 males from territories with access to fermenting banana and of 17 males from the territories without access. There was no difference in the amount of residual fat content in butterflies of two groups (t=1.17; df=31; p=0.25; Table 2). The body mass of the territorial males located in sites with exclusion cages was very similar to the body mass of males that defended the traditional non-resource sites.

The preference experiment

Of 16 territorial males given the opportunity to move to a new territory, only two abandoned the traditional sites to defend sunspots containing fermenting fruit (χ^2=9.00; p=0.003). In both cases in which a male switched to the experimental sites, the original territory was occupied by a new resident male. Among the 24 experimental sunspots used in this experiment, 10 were defended by unmarked males.

DISCUSSION

In this study we show that males of the butterfly *P. phronius* may either establish mating territories based on physical location or use the availability of fermenting fruit as an alternative cue to territory sites. Males typically defend sunny clearings along forest edges. However, numerous apparently suitable sites exist that are almost never used by butterflies. The usage of both fermenting fruit and sunny clearings without resources suggests that resource defense polygyny as well as dispersed leks are used as mate-locating tactics in this butterfly. Since males were attracted to sunspots containing fruits protected by the exclusion cages, it seems that they use both olfactory and visual or thermal stimuli to find and defend mating areas.

Resource defense systems are common in many arthropod groups, although in the great majority of species, males defend oviposition instead of feeding locations (Alcock & Houston 1987; Emlen 1997; Blanckenhorn et al. 2003; Córdoba-Aguilar & Cordero-Rivera 2005; Buzatto & Machado 2008). Among butterflies, the defense of feeding areas for mating purposes seems rare. In *Lycaena hippotoe* (Fischer & Fiedler 2001) and *L. phlaeas* (Suzuki 1976), males apparently defend concentrations of flowering plants. Because these highly aggregated resources were visited by females, males that stationed themselves near flowers could increase their reproductive success. Moore (1999) has also described males of the satyrine genus *Mycalesis* defending both areas containing soft fermenting fruit and specific perch sites along dry river beds. However, there is no suggestion that they might represent basically different behaviors or the factors that potentially drive the usage of one or other tactic.

Theory suggests that the evolution of alternative mating behaviors and their effectiveness in finding mates in butterflies should be strongly affected by the temporal and spatial distribution of females (Emlen & Oring 1977; Rutowski 1991). When females are spatially aggregated, males should benefit by defending females or the resources used by them. However, if female occurrence is unpredictable and rare, territorial mating systems without resources should be favored. Females of *P. phronius* lay eggs during all year long on abundant grasses that are widely scattered across the study site. In addition, new born females seem to require some days before becoming sexually receptive (Peixoto & Benson 2009). Since these characteristics avoid the spatial and temporal prediction of emergence sites, the evolution of the non-resource based territorial systems described for this species can be favored. Decomposing fruits, on the other hand, may be a resource with a highly patchy distribution, but short temporal availability. Because fermenting fruit represent a feeding source for both sexes (Peixoto & Benson 2009), males that establish themselves near rotting fruit may incur a higher encounter frequency with sexual partners them rivals that wander through the environment (Alcock & Houston 1987).

Regarding the comparison between male *P. phronius* at traditional and experimental sites, the greater body mass of males adopting the defense of areas with resources could suggest that they are in better conditions than individuals located in the traditional sites and consequently have greater chances to acquire high quality territories (Peixoto & Benson 2008). However, the resource access experiment showed that males feed on the baits and this caused their increase in body mass, but not in residual fat content. Additionally, if wing area is someway correlated with body mass (Peixoto & Benson 2008), the tendency is for larger males to defend sites without resources. Therefore, it is not clear if males located at non-resource or resource based sites differ in fighting ability.

In species which males show distinct mate-locating tactics, it is common that one strategy returns fewer matings then the other (Wickman 1985; Groddeck et al. 2004; Bergman et al. 2007). The preference of *P. phronius* males to stay defending sites without resources, even when unoccupied resource-based sites were available, suggests that the dispersed lek may be the higher profitable tactic. Alternatively, it may be possible that the experimental sites created during the preference experiment lacked some essential feature to attract males or that male *P. phronius* do not change their territories once established in some area. However, the defense of ten experimental sites by non-marked individuals and the fact that two marked males changed from the traditional to the experimental territories weaken these possibilities.

Because the traditional territories do not contain any evident resources used by females, it is expected that they visit such places just for copulation, whereas areas with resources may be also visited by maturing or fertilized females that are searching for food (Wickman 1985; Alcock & Houston 1987). This difference between the arrivals of sexually receptive females may be sufficient to define the preference of males to defend areas without resources. However, because territorial males located in areas with fermenting fruit feed on this resource, it is possible that they live for longer periods or increase their viability (Lederhouse et al. 1990) when compared to males that defend the traditional sites. If this occurs, the lifetime mating success of both tactics may be similar.

Understand the nature and the factors responsible for the origin and maintenance of alternative mate-locating tactics is an important step to clarify the evolution of different mating systems (Emlen & Oring 1977; Wickman 1992; Shuster & Wade 2003). Although the two alternative territorial behaviors described for male *P. phronius* seem to be uncommon in butterflies (and among insects in general), sporadic observations indicate that other satyrine species may present similar tactics. There is a good knowledge of the reproductive behaviors and a preliminary phylogeny is available for this subfamily (Kane 1982; Jones & Lace 1992; Braby

1996; Gotthard 1999; Kemp & Wiklund 2001; Merckx & Van Dyck 2005; Peixoto & Benson 2008). In this sense, the further detailing of mate-locating tactics and of how behavioral flexibility is expressed in species living under different circumstances may make the Satyrinae subfamily a good model for elucidating the origins of resource and non-resource based territorial mating systems.

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DISCUSSÃO GERAL

Os padrões descobertos para as três espécies de satiríneos investigadas nesta tese nos fornecem informações importantes acerca da compreensão dos processos envolvidos na resolução de conflitos territoriais entre machos. Porém, mais importante que isso, tais resultados incitam uma série de novas questões relativas à evolução dos sistemas de acasalamento e de sua relação com a adoção de diferentes comportamentos agonísticos.

Dependendo do nível de competição entre os machos, a intensidade dos confrontos deve variar (Emlen & Oring 1977; Riechert 1998). Se os benefícios da vitória ou os custos da derrota são extremamente elevados, ambos os machos devem investir muito nas disputas. Em casos extremos, se a única forma de adquirir parceiros sexuais depende da aquisição de um território de acasalamento, machos devem estar dispostos a brigarem até a morte (Enquist & Leimar 1990). Como grande parte das características que potencialmente afetam a intensidade de competição variam no tempo ecológico (Fig. 1) e dependem da interação entre características ambientais e biologia dos organismos, não há uma forte razão para presumir que espécies relacionadas (ou mesmo populações distintas) apresentem sistemas territoriais idênticos. O capítulo 1 representa um exemplo ideal nesse contexto, uma vez que *H. hermes* e *M. soter* são morfologicamente similares, ocorrem no mesmo ambiente, mas apresentam disputas que são resolvidas de formas distintas.

Mais interessante ainda é o fato de que as disputas não são satisfatoriamente explicadas por nenhum dos modelos atuais sobre a resolução de conflitos. Enquanto para *H. hermes* brigas decididas com base na capacidade de persistência parecem ser a regra, para *M. soter* o padrão ainda é obscuro. Duas vias de pesquisa podem se desenvolver a partir desses resultados. Por um lado, novos modelos sobre resolução de conflitos podem ser propostos. Alguns trabalhos recentes têm demonstrado que modelos relativos aos conflitos sexuais pecam ao não considerarem variáveis populacionais (Kokko & Rankin 2006). Em especial, modelos que contraponham os benefícios relativos à adoção de táticas não territoriais de acasalamento com as táticas territoriais comumente adotadas em uma população, podem representar um novo avanço para o entendimento dos comportamentos exibidos ao longo das disputas. Na outra via, trabalhos que busquem identificar relações causais entre as características dos machos e sua função na geração de custos ao longo das disputas fornecerão importantes avanços empíricos para o teste dos modelos existentes (Lailvaux & Irschick 2007). Muitos trabalhos têm encontrado diferenças morfológicas e fisiológicas entre machos vencedores e perdedores de confrontos (Forsyth & Montgomerie 1987; Alcock & Bailey 1997; Fitzstephens & Getty 2000; Briffa & Elwood 2001; Kemp 2002; Peixoto & Benson 2008). Porém, ainda não é possível afirmar quais dessas características participam efetivamente na geração de custos e quais representam apenas subprodutos das características funcionalmente relevantes para a capacidade de luta.

O capítulo 2 é particularmente interessante ao revelar que, para indivíduos de uma mesma população, características diferentes podem ser identificadas como importantes para a resolução dos conflitos dependendo do contexto no qual elas foram investigadas. Enquanto apenas residência prévia é importante para a resolução de conflitos nos quais os machos tenham papéis claramente separados em residentes e intrusos, massa corporal passa a ter um papel chave na distinção de indivíduos perdedores e vencedores em conflitos nos quais ambos os adversários foram induzidos a se comportarem como residentes. Neste caso, aparentemente tanto o valor do recurso (relativo à residência prévia), quanto as características dos machos podem afetar o resultado de um confronto.

Se contrapusermos os resultados do capítulo 2 com os do capítulo 1, o questionamento do papel funcional das características dos machos sobre a resolução dos conflitos se torna evidente. Enquanto no capítulo 1 gordura e idade separaram machos residentes de machos intrusos, no capítulo 2 apenas a massa corporal foi importante nas chances de vitória em uma disputa. Será que machos residentes são mais fortes por estocarem maior quantidade de gordura ou será que a gordura é acumulada porque machos residentes permanecem mais tempo pousados que machos não residentes? Será que a taxa de desgaste alar dos machos residentes é simplesmente menor que a dos machos intrusos? Ainda, se massa corporal é realmente importante na resolução de conflitos que não apresentam contato físico, qual o papel dela na geração de custos? Machos mais pesados têm melhor condição, são menos parasitados ou as disputas podem, em alguns casos, escalonar até fases com contato físico intenso? Trabalhos extremamente interessantes podem ser originar a partir destas perguntas.

Finalmente o capítulo 3 nos revela que os comportamentos de encontro de parceiros sexuais exibidos pelos machos podem ser extremamente versáteis. Enquanto alguns machos se estabelecem em locais sem recursos, outros podem defender áreas de forrageio, gerando em uma mesma população um lek e um sistema poligínico com defesa de recursos. Além disso, existem ainda outros machos que não conseguem defender nenhum território e vagam no ambiente em busca de fêmeas ou de sítios de acasalamento vagos (Peixoto & Benson 2008). No entanto, resta entender até que ponto a existência dessas duas alternativas territoriais e uma não territorial pode influenciar os confrontos pela posse de sítios de acasalamento. Compreender o papel das fêmeas se torna crucial nesse ponto. Uma vez que machos podem alternar entre diferentes táticas de acasalamento, é provável então que todas assegurem alguma chance de cópula. Mas será que existe alguma diferença no sucesso de machos com táticas distintas? Se a diferença for pequena, isso pode justificar brigas pouco intensas, já que machos perdedores podem lucrar mais ao investir em outros meios de encontrar parceiras sexuais.

Por sua variedade nos sistemas de acasalamento (Knapton 1985; Heinrich 1986; Wickman 1992; Jones & Lace 1992; Alcock 1994; Braby 1996; Moore 1999; Gotthard 1999; Peixoto & Benson 2009), nas estratégias empregadas durante as disputas territoriais (Davies 1978; Kane 1982; Wickman 1985; Rosenberg & Enquist 1991; Stutt & Willmer 1998; Kemp et al. 2006; Peixoto & Benson 2008) e pelo bom conhecimento acerca de sua filogenia (Peña et al. 2006), a subfamília Satyrinae se mostra como um modelo de estudo promissor para que possamos compreender melhor como processos ecológicos e evolutivos atuaram na geração dos diferentes sistemas de acasalamento em insetos. Diversas espécies temperadas desse grupo possuem estudos comportamentais extremamente detalhados e, em breve, espero que possamos adicionar algumas espécies presentes no Brasil a esse quadro.

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